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Cracidae (Aves, Galliformes)

by FRANÇOIS VUILLEUMIER

RELATIONSHIPS AND EVOLUTION WITHIN THE CRACIDAE (AVES, GALLIFORMES)[1]

FRANÇOIS VUILLEUMIER

INTRODUCTION

The latest systematic treatments of the Cracidae by Peters (1934), and by Hellmayr and Conover (1942), showed no real improvement over the older one by Sclater and Salvin (1870). All recent authors who have dealt with the Cracidae have done so in the course of regional faunal studies, reviewing only part of a genus or a species without consideration for variation in the total range of the taxon. This is also true for other groups of neotropical birds. The only original studies on Cracidae that brought new and much needed data on ecology and behavior were by Wagner (1953) on Mexican, and by Schäfer (1953) on Venezuelan species.

During an investigation of speciation patterns in the Cracidae, I first undertook a character analysis to re-evaluate generic limits within the family. This led to an arrangement slightly at variance with the classifications of Peters and of Hellmayr and Conover. Within each genus, inter- and intraspecific variations were then studied to determine the stage of the speciation process, evaluating thus the significance of morphological differentiation. Finally, a review of the existing forms and their distribution, coupled with the fossil record, served as a

basis for a reconstruction of the origin and evolutionary sequence leading to the modern species of the genera *Penelope* and *Crax*.

I must emphasize that I have not attempted a formal revision of the species of Cracidae, for two reasons. First, because whether a form is treated as a species or as a subspecies was considered irrelevant to the aims of this study; second, because much more work on museum skins, supplemented with collecting in critical areas, must be done before a definitive arrangement of the species can be reached, and before the variation within each species can be properly assessed. The list of recognized species, particularly in the genus *Ortalis*, must therefore be taken as tentative, pending the result of studies currently undertaken by others.

The concepts adhered to in this paper are those of broad genera and of the biological species, as defined by Mayr, Linsley, and Usinger (1953). In the case of allopatric, non- or slightly overlapping forms, the criteria for specific recognition are those mentioned by Mayr (1963: 345): "complete lack of intergradation in a continental area, in the absence of geographic barriers, is now taken as proof of specific distinctness."

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lems and with fossil Cracidae. Dr. Ernest Williams. Prof. Bryan Patterson. Drs. Walter J. Bock. W. John Smith. Mr. Reginald E. Moreau, and Mrs. B. P. Hall read the manuscript and suggested many improvements for which I am very thankful. I am much obliged to Drs. Philip S. Humphrey (United States National Museum), Alden H. Miller (Museum of Vertebrate Zoology, Berkeley), and Robert W. Storer (University of Michigan Museum of Zoology) for lending me skeletons of Cracidae. I must thank the officials of the Museum of Comparative Zoology for their cooperation during the course of my work, and those of the Academy of Natural Sciences of Philadelphia for kindly placing the collections at my disposal during a visit to this institution. I am grateful to Dr. Oliverio Pinto for his valuable information on the distribution of some Cracidae in Brazil. Mr. John A. Griswold has most kindly supplied photographs of *Crax mitu* and has given many useful details about these birds living at the Philadelphia Zoological Garden. Finally I want to thank Mrs. Alice J. Daniels for preparing Figures 1 through 9.

THE CRACIDAE

Various and recent kinds of evidence tend to indicate that the Cracidae are more closely related to the other groups of Galliformes (in particular to the pheasants) than has been suggested in the past (Sibley, 1960; Mainardi, 1963). The cracids differ from all other gallinaceous birds by their arboreal habits, their nests of sticks built in trees and bushes, and their clutches of 2 to 3 (rarely 4) big, rough-shelled white eggs. The majority of species are found within the limits of the American tropics; the greatest number occur in South America, particularly in the northwestern corner.

Most Cracidae live in the forest interior, some in more open situations: forest-edges and brushy habitats. Some species of curassows (*Crax*) and guans (*Penelope*) require humid conditions, such as are found in lowland rain forest and montane rain forest (cloud forest). Only a few species of cha-

chalacas (*Ortalis*) prefer drier habitats. No species is found far from trees, however, which provide them with both shelter and food. The latter is mostly vegetal, and consists of fruits, leaves, buds, vine tendrils, and an occasional insect. Several species are quite gregarious, especially after the nesting period, and loose flocks of *Penelope* or *Ortalis* can be seen feeding on fruit-laden trees.

CLASSIFICATION

Huxley (1868) divided the Cracidae on the basis of a difference in the proportions of the pelvis in some genera, concluding (p. 297): "The Penelopinae (*Penelope, Oreophasis, Ortalida*) have the postacetabular area broad; but in the Cracinae (*Crax, Pauxi*) it is narrow." Sclater and Salvin (1870) adopted this "trenchant difference," coupled with minor differences in bill shape, to distinguish three subfamilies, essentially the same as Huxley's except that *Oreophasis* was placed in a subfamily of its own. Their subfamilies were: 1) Cracinae (*Crax, Nothocrax, Mitu, Pauxi*) 2), Penelopinae (*Stegnolaema, Penelope, Penelopina, Pipile, Aburria, Chamaepetes,* and *Ortalis*), and 3) Oreophasinae (*Oreophasis*). Peters (1934) brought only minor changes in the generic arrangement of Sclater and Salvin. *Stegnolaema* was correctly assigned to *Penelope*, and the name *Ortalis* replaced *Ortalida*, since the latter seems to be the accusative of the former. He did not recognize any subfamilies, nor did Hellmayr and Conover (1942) who, while differing somewhat in the treatment of species, did not alter Peters' generic grouping. Among recent authors who revived the subfamilies are Ridgway and Friedmann (1946), and Tordoff and Macdonald (1957); Verheyen (1956) subdivided the family into four tribes: Cracini, Oreophasini, Penelopini, and Pipilini.

I have restudied the osteological difference cited by Huxley and have been able to confirm his findings. I examined the following species (number of skeletons in parentheses): *Ortalis vetula* (4), *O. ?gar-*

rula (1), *O. ruficauda* (1), *Chamaepetes unicolor* (1), *Penelopina nigra* (2), *Penelope purpurascens* (4), *Crax urumutum* (1), *C. salvini* (1), *C. tomentosa* (2), *C. mitu* (3), *C. fasciolata* (4), *C. alberti* (1), *C. alector* (2), and *C. rubra* (5). On the basis of measurements of total pelvic length, length of the preacetabular area, length of the postacetabular area, and width of the postacetabular area, it appears that the postacetabular area is relatively broader and shorter in *Ortalis, Chamaepetes, Penelopina,* and *Penelope* than in *Crax*. It seems, however, that Huxley emphasized this difference without enquiring into its possible significance. As a rule, birds with more terrestrial habits tend to evolve a proportionately longer pelvis than birds of more arboreal habits (B. Patterson, pers. comm.). This probably applies to the Cracidae, where the more terrestrial *Crax* have a relatively longer pelvis than the more arboreal *Ortalis, Chamaepetes,* and *Penelope* (the rather terrestrial *Penelopina* being an exception). The adaptiveness of this difference in pelvic proportions, and further the very close relationships within the Cracidae do not, in my opinion, justify a subdivision of the family into subfamilies or tribes.

My main disagreement with the classifications of Peters, and of Hellmayr and Conover, concerns the generic limits in the curassows: as I explain later in more detail, I see no reason to maintain *Nothocrax, Mitu,* and *Pauxi* as separate genera; all the curassows are united under the generic name *Crax*. Similarly, I am convinced that *Pipile* belongs in *Penelope*, of which it should become a synonym. *Aburria* and *Chamaepetes* are kept as separate genera for lack of better evidence, but their close relationship to *Penelope* is indicated by their position in the list. *Penelopina* is also kept separate, but its intermediate position between *Penelope* and *Ortalis* must be emphasized. Insofar as possible, the sequence of genera expresses the degree of relationship and the amount of specialization (from least to most specialized). Thus it differs considerably from Peters' and Hellmayr and Conover's sequence.

In the main, Hellmayr and Conover's species limits have been accepted, except for the following: *Ortalis columbiana* is here considered a full species, on the authority of Miller (1947, 1952), and not a subspecies of *guttata*. *Ortalis poliocephala* and *O. vetula* are considered distinct species, on the basis of field data from Wagner (1953) (see also Moore and Medina, 1957). Pending further evidence, *O. leucogastra* is retained as a subspecies of *vetula*. The close relationships of the *Ortalis poliocephala-vetula-ruficauda-ruficrissa* complex are indicated by treating them as members of a superspecies. *Ortalis wagleri* is considered conspecific with *poliocephala* (Moore and Medina, 1957). *Penelope cujubi* and *jacutinga* are treated as subspecies of *pipile*. Similarly *Penelope ochrogaster* and *pileata* are merged with *jacucaca*. *Penelope jacquaçu, P. granti,* and *P. obscura* are considered conspecific with *P. purpurascens*. *Penelope albipennis* is believed to be a color variant of *ortoni*, and *ortoni* is treated as a subspecies of *P. montagnii*. *Crax unicornis* is treated as a subspecies of *C. pauxi*, as already done by Wetmore and Phelps (1943).

The classification outlined below is based on the various kinds of evidence later discussed in detail; it is presented at this time for uniformity of nomenclature throughout the paper. Superspecies, as defined in Mayr (1963: 499, 672) are included in braces.

CLASSIFICATION OF THE CRACIDAE

Genus *Ortalis* Merrem 1786

> *motmot* (Linnaeus)
> *superciliaris* (Gray)
> { *guttata* (Spix)
> { *columbiana* Hellmayr
> [*poliocephala* (Wagler)
> { *vetula* (Wagler)
> { *ruficrissa* (Sclater and Salvin)
> [*ruficauda* (Jardine)
> *garrula* (Humboldt)
> *erythroptera* (Sclater and Salvin)
> *canicollis* (Wagler)

Genus *Penelopina* Reichenbach 1862

> *nigra* (Fraser)

Genus *Penelope* Merrem 1786
    1) *pipile* species-group
             { *pipile* (Jacquin)
             { *cumanensis* (Jacquin)
    2) *jacucaca* species-group
             jacucaca Spix
    3) *purpurascens* species-group
             purpurascens Wagler
    4) *montagnii* species-group
             montagnii (Bonaparte)
             marail (P. L. S. Müller)
             argyrotis (Bonaparte)
             superciliaris Temminck

Genus *Aburria* Reichenbach 1852
             aburri (Lesson)

Genus *Chamaepetes* Wagler 1832
             { *unicolor* Salvin
             { *goudotii* (Lesson)

Genus *Oreophasis* Gray 1844
             derbianus G. R. Gray

Genus *Crax* Linnaeus 1758
    1) *rubra* species-group
             { *rubra* Linnaeus
             { *globulosa* Spix
             { *alberti* Fraser
             { *annulata* Todd
             { *daubentoni* G. R. Gray
             fasciolata Spix
             blumenbachii Spix
             alector Linnaeus
    2) *mitu* species-group
             { *mitu* Linnaeus
             { *salvini* (Reinhardt)
             { *tomentosa* Spix
             pauxi Linnaeus
             urumutum Spix

CHARACTER ANALYSIS

1) Casque

Bony structures growing as projections from cranial bones, usually the frontals, the premaxillae or the parietals, and covered in life by a horny development of the rhamphotheca, are found in many families of birds. In the Cracidae, such a casque is present and well developed in *Crax mitu* (Fig. 21), *C. pauxi* (Fig. 1), and *Oreophasis derbianus* (Fig. 2); it is absent in the other species of *Crax* and in the other genera.

The size of the casque varies during the life of the bird. In the young *Crax mitu*, the bill is almost normal and presents only a slightly flattened and elevated culmen, contrasting with the enormous and bulbous casque of the adult, especially of the male (Fig. 21). In life, the horny covering of the casque is brightly colored: orange-red in *Crax mitu*, blue in *C. pauxi*, and red in *Oreophasis derbianus*. It is noteworthy that in other species of *Crax*, that lack a bony casque, there is either a fleshy knob, usually red or yellow, or a brightly colored rhamphotheca.

It is very likely that structures like a bony casque and a fleshy protuberance can evolve relatively rapidly, perhaps under selection pressures that place emphasis on species-specific characters, which the birds themselves might well use as identifying marks. This idea of rapid evolution of such structures is strengthened by their conspicuous variation in closely related species. In the *mitu* species-group, one member of a superspecies (*mitu*) has a very pronounced casque, while this structure is altogether absent in *tomentosa* (Fig. 3), and represented by a flattening of the dorsal surface of the culmen in *salvini* (Fig. 4). In other birds, a parallel case is observed in pigeons of the genus *Ptilinopus*; *P. iozonus* and *P. insolitus* are the two morphologically very similar members of a superspecies: *iozonus*

Fig. 1. Lateral view of the head of *Crax pauxi*, to show the size of the casque of an adult bird.
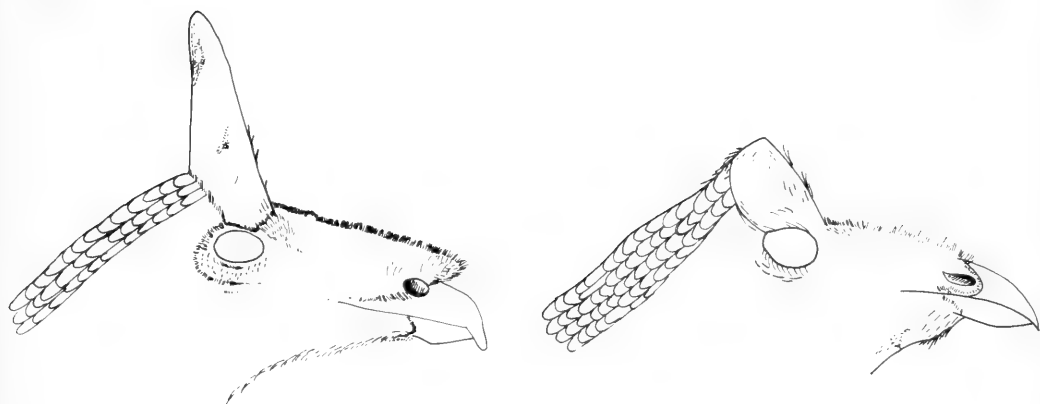
Fig. 2. Variation in the size of the casque of *Oreophasis derbianus*. Left: fully developed, and right: partly developed casque.

(no casque) inhabits New Guinea, the western Papuan Islands and the Aru Islands, and *insolitus* (with casque) is found on the Bismarck Archipelago (Cain, 1954).

That the casque and fleshy protuberance are no more than species-specific recognition marks is further suggested by the function of the white frontal shield of the coot *Fulica americana*. The shield is an extension of the rhamphotheca over the forehead, surmounted by the reddish callus. Gullion (1951) succeeded in producing larger shields by implanting testosterone subcutaneously. He showed that the shield is used in aggressive territorial displays, and that "paired birds are able to recognize their mates by the shape of the callus."
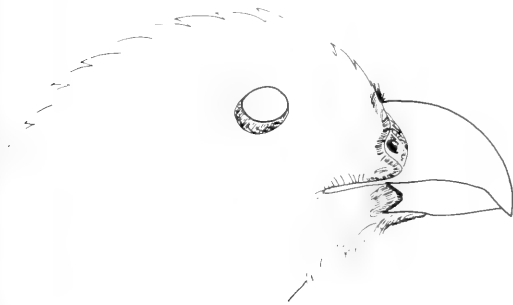
Fig. 3. Lateral view of the head of *Crax tomentosa*. This species has neither casque nor elongated crest feathers.

2) Crest Feathers

All birds of the genus *Crax*, except *tomentosa* and *pauxi*, have elongated and erectile crest feathers (see Fig. 21, showing adult *C. mitu* with flattened feathers and young with erected feathers). In the *rubra* species-group these feathers are curled forward. Three species, *mitu*, *salvini*, and *urumutum* (see Fig. 21, and Figs. 4 and 5) have elongated but not curly crest feathers. In *Penelope* the crest feathers are erectile and straight (see Fig. 6), sometimes short, and only slightly longer than ordinary feathers of the pileum. In the *pipile* and *jacucaca* species-groups, however, the feathers are more elongated and have fewer barbs (decomposed) than in other species, and are also more conspicuously colored. All other cracids have ordinary short crest feathers.

There is a tendency for an inverse correlation between the presence of elongated crest feathers and the occurrence of wattles or areas of naked skin on the throat. Most species of *Crax* have long crest feathers, but only a few have a wattle (on the lower mandible), while in other genera, particularly *Ortalis*, *Aburria*, most species of *Penelope*, and *Penelopina*, the birds have wattles or areas of naked skin on the throat or both, but short crest feathers.
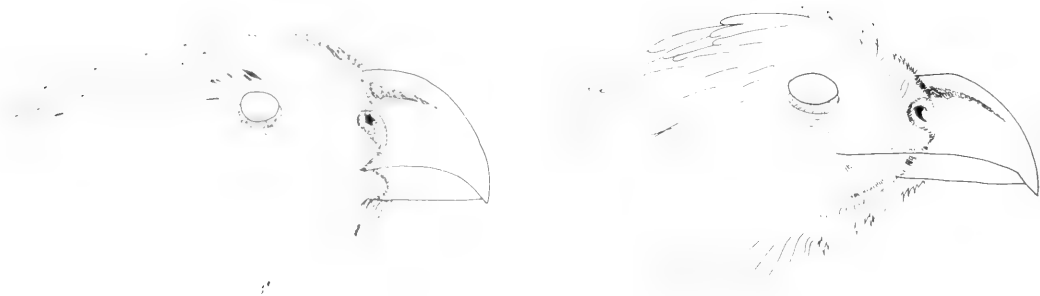
Fig. 4.   Variation in the size of the bill in *Crax salvini*. Left: male. Right: female. This species has elongated crest feathers (like *C. mitu*) and a bill intermediate in size between *C. mitu* (with casque), and *C. tomentosa* (no casque).

There is some evidence that crest feathers serve as signals, merely aiding the territorial proclamation of the calls. For instance, *Penelope purpurascens aequatorialis*, which has moderately short crest feathers, erects them and displays the red color of the throat during its call (Schäfer, 1953).

3) Wattles

In the Cracidae wattles occur in the following genera: *Crax* (swellings on the lower mandibles, yellowish or greenish in color), *Penelope* (red or purplish area of naked skin on the throat, extended as a dewlap, Figs. 6 and 7), *Aburria* (long, hanging yellow wattle, Fig. 8), *Penelopina* (orange colored dewlap in the male only, Fig. 9), and *Ortalis* (red area of naked skin on the throat). In addition, quite a number of species have a more or less extensive area of naked skin around the eye, called an "eye-wattle."

As pointed out by Mayaud (1950) the dermis of wattles and areas of bare skin, especially those without pigmentation, possesses an intense vascularization, and during the period of sexual activity the structures increase in development or coloration by increase in vascularization under the influence of endocrine secretion. This might also be true of the Cracidae where an increase of color intensity has been described in the frontal protuberance of *Crax rubra* (Sutton, 1955), in the areas of naked skin of *Oreophasis derbianus* (Wagner, 1953),

and in the dewlap of *Penelopina nigra* (Wagner, 1953).

In the Cracidae, as well as in the Casuariidae (Mayr, 1940: 2), the Phasianidae (Delacour, 1951: 123), and the lapwings *Vanellus* (Bock, 1958: 47), the wattles vary in shape, size, and color from species to species, and also intraspecifically.

The Cracidae are too little known in nature to be certain of the function(s) of wattles. Judging from the observations of Schäfer (1953) cited earlier, on the display of the red naked skin of the throat by *Penelope purpurascens aequatorialis*, and judging by the uniformity of shape and color of the wattles in the genera *Ortalis* and *Penelope*, it is likely that wattles are not used in courtship in these birds but, as suggested before for the casque and frontal protuberance, in territorial signaling. The only species in which the wattle is quite different from that of other cracids is

Fig. 5.   Lateral view of the head of *Crax urumutum*.

Aburria aburri, but its display functions are not known.
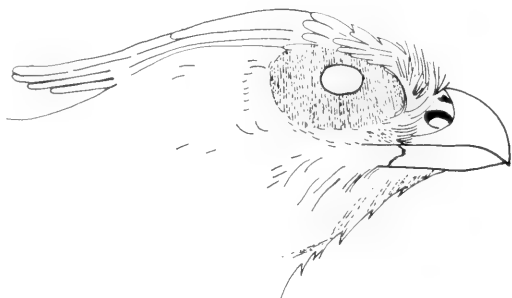
4) Attenuated Primaries

Both sexes of *Chamaepetes unicolor, C. goudotii, Aburria aburri, Penelope pipile,* and *P. cumanensis* have the two or three outer primaries attenuated. A similar modification is also seen in *Penelope argyrotis columbianus,* less so in *P. superciliaris,* and hardly at all in *P. montagnii sclateri.* That such a modification is connected with sound production in a special form of flight display ("drumming") is known definitely in *P. cumanensis,* and almost certain also for *Chamaepetes* and *Aburria.* It is very interesting, however, that drumming flights have been reported in species which have normal outer primaries like *Penelope purpurascens* (Sutton and Pettingill, 1942), and *Penelopina nigra* (Salvin and Godman, 1901). This suggests that attenuation serves to modify or amplify the sounds produced with normal feathers. Although accurate voice descriptions are lacking for all species that have attenuated outer primaries, there may be some correlation, as suggested by the fact that there is no tracheal curvature in *Penelope pipile, P.*
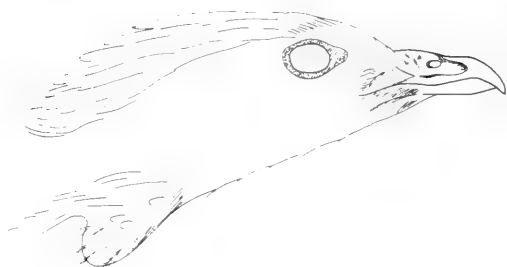
Fig. 7. Lateral view of the head of *Penelope pipile jacutinga* showing the dewlap.

cumanensis, P. purpurascens, and *Aburria aburri.*

In birds other than cracids, attenuated primaries may be present or absent in closely related species, as in the genus *Falcipennis* of the Tetraoninae. The Asiatic species *F. falcipennis* has modified primaries, while the North American one, the Spruce Grouse *F.* ("*Canachites*") *canadensis,* does not. Such a difference also occurs, for instance, in some Tyrannidae. "The male [of *Euscarthmornis g. granadensis*] was heard giving a wing buzz suggestive of a manakin; this undoubtedly is produced by the especially attenuate four or five outer primaries. Such a modification of the primaries is not evident in *Euscarthmornis margaritaceiventris,* a number of specimens of which are at hand" (Miller, 1963: 32). It is obvious, then, that a character such as the attenuate condition of the primaries in some birds would be only of specific value taxonomically.

5) Tracheal Loop

Convolutions of the trachea over the pectoral musculature occur in several groups of birds. Garrod (1879) listed some cracid species presenting this particularity, and Forbes (1882) mentioned many more. Further notes on cracid tracheal morphology were included by Wetmore (1926), Miller (1947, 1952), Wagner (1953), and Schäfer (1953).

In *Crax* the tracheal loop is evident in the male only, and in *C. daubentoni* (Schäfer, 1953) the loop seems absent outside of

Fig. 6. Lateral view of the head of *Penelope purpurascens* with erected crest feathers. Drawn from a photograph of a captive bird.

Fig. 8. Lateral view of the head of *Aburria aburri* with the throat wattle.

Fig. 9. Lateral view of the head of *Penelopina nigra*, male, showing the dewlap.

the breeding season (this would deserve more investigation). In *Penelope* the trachea is simple in both sexes of *purpurascens* (Garrod, 1879), *pipile*, and probably also *cumanensis* (Forbes, 1882), and in the male of *montagnii ortoni* (pers. obs.). The trachea is convoluted in both sexes of *P. jacucaca pileata* and *P. jacucaca jacucaca* (Forbes, 1882) and in (sex?) *P. argyrotis* (Schäfer, 1953). The trachea is simple in both sexes of *Aburria aburri* (Forbes, 1882). In *Ortalis* a convoluted trachea is an attribute of the male in all species examined so far: *motmot*, *guttata*, *garrula* (Forbes, 1882), *columbiana* (Miller, 1947, 1952), *vetula* (pers. obs.), and *ruficauda* (Schäfer, 1953).

It would be instructive to know fully the interrelationships of tracheal morphology, voice, and drumming flights. Although the data are quite incomplete they suggest the following correlations. 1) A deep, booming voice is produced by the males (all having a convoluted trachea) of *Crax pauxi*, *C. rubra*, and *C. alector*; none has a drumming flight. 2) In *Penelope pipile*, *P. cumanensis*, and *Aburria aburri* the trachea is simple and the primaries attenuated. At least one of these (*P. cumanensis*) is known to have a drumming flight. The voice is practically unknown so that further correlation is not possible. 3) In *Ortalis*, where a tracheal loop is only present in the males, the birds emit the raucous and noisy calls which gave them their local names (onomatopoetic) of chachalacas (in Mexican species), charatá

(*O. canicollis*, Wetmore, 1926), guacharaca (*O. ruficauda*, Friedmann and Smith, 1950), wakagó (*O. motmot*, Haverschmidt, 1956). None has a drumming flight.

6) Color Pattern

"In some natural groups of birds the beak, feet, or structure of the feathers may show extraordinary variability while the colour pattern remains very constant" (Cain, 1954: 268). This has been demonstrated also in the lapwings of the genus *Vanellus* (Bock, 1958). In the Cracidae, this is particularly evident in the curassows of the genus *Crax*. These birds have (at least in the males) black body plumage, except on the upper part of the thighs, the lower belly, and the undertail coverts, which are either white or chestnut. The females of the *rubra* species-group differ usually from the males in having much brown or buff in their plumage, but their lower belly and undertail coverts are almost always brownish, suggesting the same pattern as in the males. The exception is the female of *C. alector* which differs from the male only in having white barrings in her crest feathers.

The pale belly color is believed to play a part in the displays in three species, but it is premature to assign precise significance to these ceremonies. The male of *Crax*

rubra "raises the tail vertically and lowers the feathers of the breast to form a sort of hanging plastron, at the same time displaying the white feathers of the belly and withdrawing the head in the shoulders" (translated from Alvarez del Toro, 1952: 124). In *Crax alector* "the entire body is tilted far forward, the breast low and the wings pointing down in front, the wrist portion . . . dropping almost to the ground. The wing tips lie flat upon the back, and the tail is raised, while the head is held high, almost touching the back and tips of the wings. The tail, carrying out the line of the back, points straight upward, and the white belly, flanks, and especially the undertail coverts are fluffed out to their greatest extent, forming a most conspicuous white mark against the black of the remaining plumage" (Beebe and Beebe, 1910: 334–337). The bird then emits snorts, picks up pebbles, or small objects, and strikes its head with force against its back. This is followed by the dropping of the pebbles, clapping of wings over the back, and finally emission of the booming sound. Schäfer (1954: 120) describes a fright reaction in *Crax pauxi* where "the long tail is raised by jerks, whereby the beautiful silvery tips become visible" (translated). Since, however, Schäfer (1953) remarks on the absence of elaborate ceremonies in this species, it is quite possible that they occur only in cracids that are sexually dimorphic and monogamic like *C. rubra*, or hardly dimorphic but polygamic like *C. alector.*

Alone among the members of the genus *Crax*, the species *urumutum* does not have any black in its plumage. The black is replaced by mottled brown, and the paler lower belly is uniform buff. Thus, the same pattern is visible, though not so obvious, as in the other species. Other characters such as bill shape, crest feathers, and tracheal loop, all point to its close relationship with other species of *Crax*, especially of the *mitu* species-group.

In the genus *Penelope*, the *pipile* and *jacucaca* species-groups differ somewhat

from the other species-groups in color pattern. The most conspicuous difference lies in the color of the crest feathers: white in *pipile*, brown in *jacucaca*, in both cases paler and in contrast with the color of the rest of the plumage. In the other species-groups the crest feathers are the same color as the neck and most of the body plumage. The broad white patch on the wing of *pipile* is subject to extensive individual variation, and can be much reduced in some birds producing an effect not very different from the white spotting of other species of *Penelope.*

Aburria aburri and the two species of *Chamaepetes* all have uniform black or brown coloration, thus differing somewhat from *Penelope*. They are more generalized than any species of the genus *Penelope*, without erectile crest feathers, and without wattles or areas of naked skin in *Chamaepetes.*

Of all cracids *Oreophasis* is the only one to have a peculiar plumage pattern, with a conspicuous white bar across the middle of the tail, and white plumage on the breast.

DISCUSSION OF CHARACTERS

Wing (1946) brought together information on the courtship performance of North American species of Tetraoninae, showing the correlations between morphological characters such as erectile feathers and throat sacs, and behavioral ones such as dancing and drumming. It is probable that when the Cracidae are better known a similar analysis will be feasible. At present only some comments are possible.

1) A casque or a frontal protuberance is present in most species of *Crax*. This structure is always brightly colored, usually yellow or red, more rarely greenish or bluish. The species that have no casque have a red or yellow bill. Long crest feathers are found in most species of the genus, the exceptions being *C. pauxi* (casque) and *C. tomentosa* (no casque). The trachea is convoluted in the males only. The voice is deep, described by various authors as

"hoots," "booming," etc. (exception: *C. daubentoni*, see Schäfer, 1953). There is evidence that loud calling is done only by the males and that it has territorial functions. Tracheal structure and voice, as well as color pattern, exhibit a remarkable uniformity throughout the genus. Close relationship of the species is suggested by the almost complete lack of genetic isolating mechanisms (postmating mechanisms of Mayr, 1963: 92) shown in hybridization experiments in captivity, as explained later. It seems that the species of the genus *Crax* are in a stage of the speciation process where ecological and ethological isolation in the narrow zones of overlap is sufficient to prevent interbreeding (premating mechanisms (a) and (b) of Mayr, 1963: 92).

2) All species of the genus *Penelope* have a wattle, in the form of a dewlap or an area of naked skin on the throat. All species have erectile crest feathers used apparently in connection with the wattle, possibly during the territorial calling, as reinforcement of signal characters. The tracheal structure varies, from species lacking convolutions in both sexes to species that have them in both sexes. There is an apparent correlation between species with a simple trachea and a special drumming flight, the significance of the latter being as yet obscure.

3) The only species of *Penelopina* is much more sexually dimorphic than any other species in the other genera, and there is no pair bond (Wagner, 1953). Flight of the drumming kind and voice similar to that of *Ortalis vetula* (Pitelka, cited by Leopold, 1959) have been described and make *Penelopina nigra* somewhat intermediate between *Penelope* and *Ortalis*, but maybe still distinct enough to be maintained in a different genus.

4) *Ortalis*, like *Crax*, exhibits a great uniformity in several characters, such as plumage pattern, voice, tracheal structure, and tendency to polygamy. There is no question as to the limits of the genus.

5) To sum up, it is evident that characters such as the casque, relied upon heavily in the past to establish genera, are only of specific value; there is thus no reason to keep *Nothocrax*, *Pauxi*, and *Mitu* separate from *Crax*, where they undoubtedly belong. In *Crax*, color pattern, voice, and tracheal structure are much better clues to the relationships than wattles and/or casque. In *Penelope*, there is much more variation in color pattern, as shown by the *pipile* species-group, and there is also more variation in tracheal structure. It becomes thus more difficult to give diagnostic characters for the genus. The throat wattle seems to vary less throughout *Penelope* than other characters. On the basis of such evidence it is unnecessary to maintain a separate genus for the *pipile* superspecies, which is only a distinct species-group within *Penelope*. It is possible that after more study, *Aburria* and *Chamaepetes* will be also included there.

HYBRIDS

As far as I know no cracid hybrid has ever been reported in nature. All the cases mentioned in the literature concern hybrids obtained in captivity (Gray, 1958). Even in southern México where *Ortalis vetula* and *O. poliocephala* are sympatric (Wagner, 1953), or in the Upper Sinú Valley of northern Colombia, where *Crax rubra* and *C. alberti* have been found in the same area (Blake, 1955), no intergradation seems to take place. The latter case is quite interesting in view of hybrids produced in captivity between *C. alberti* and *rubra* (Taibel, 1950). Other crosses include *C. alberti* × *C. fasciolata* (Bronzini, 1940, 1946), and *C. alector* × *C. rubra* (Ackermann, 1898; Przibram, 1910), and concern broadly allopatric forms. Taibel (1961 a,b) crossed *Crax alberti* and *C. mitu* and found the F_1 and F_2 hybrids to be completely fertile, as well as the offspring of the backcrosses. In *Penelope*, F_1 hybrids were obtained between *marail* and the rather different *jacucaca pileata* (Hopkinson, 1926, 1939).

TABLE I.   FOSSIL CRACIDAE

FOSSIL	FORMATION	TIME	LOCALITY	AUTHOR
Ortalis phengites	"Upper Snake Creek Beds"	Pliocene	South of Agate, Sioux Co., Nebraska	Wetmore (1923)
Boreortalis laesslei	Hawthorn Formation, Thomas Farm local fauna	Lower Miocene	Thomas Farm, Gilchrist Co., Florida	Brodkorb (1954)
Ortalis pollicaris	Rosebud Formation	Lower Miocene	Flint Hill, 9 miles west-south-west of Martin, Bennett Co., South Dakota	Miller (1944)
Ortalis tantala	Harrison Formation	Lower Miocene	Carnegie Hill, Sioux Co., Nebraska	Wetmore (1933)
Palaeonossax senectus	Brule Formation, Poleslide member	Upper Oligocene	5 miles south of Scenic, South Dakota	Wetmore (1956)
Procrax brevipes	Chadron Formation, Peanut Peak member	Lower Oligocene	Pennington Co., South Dakota	Tordoff and Macdonald (1957)
Gallinuloides wyomingensis	Green River Formation	Middle Eocene	Fossil, Wyoming	Eastman (1900)

True intergeneric hybrids were produced between *Crax rubra* and *Penelope jacucaca pileata*, but when adult the birds did not show any sexual activity (Poulsen, 1949, pers. comm. cited by Gray, 1958). Furthermore, *Ortalis guttata* and *Gallus domesticus* "are said to cross readily" (Gray, 1958).

From this evidence of hybridization in captivity but not in nature, it appears that allopatric populations have reached a stage of speciation where morphological differentiation and also ecological divergence have taken place in isolation so that, as in the Francolins *Francolinus* "interbreeding is unlikely (but not impossible) if the two populations rejoin" (Hall, 1963).

FOSSIL CRACIDAE[1]

Seven fossil cracids have been described in the literature. The oldest, *Gallinuloides wyomingensis*, from the Green River shales of Fossil, Wyoming, attributed to the Middle Eocene, was placed by Lucas (1900) in a family Gallinuloididae mostly because of the absence of a well-developed post-angular process. Professor Bryan Patterson and I have re-examined the type but cannot be satisfied that the process is actually lacking or that it was broken off. As Tordoff and Macdonald (1957) rightly pointed out, however, the process "does not seem to be a valid basis for establishment of a separate family." I agree with them that *Gallinuloides* belongs in the Cracidae.

Procrax brevipes is the only other fossil of the family known from more than a bone fragment. In their careful study, Tordoff and Macdonald (1957) compared *Procrax* with a number of modern genera. On the basis of their description there seems to be no doubt that *Procrax* is a valid genus, but I would question putting it into a subfamily together with *Gallinuloides*. In view of its numerous similarities to modern cracids,

[1] After this paper was completed, I learned of Brodkorb's Catalogue of Fossil Birds, Part 2 (Bull. Florida State Mus., 8 (3): 195–335, 1964) in which a number of fossil birds were removed from various families and referred to the Cracidae. If these changes are accepted, it means that cracids were present in France from the Upper Eocene to the Lower Miocene, in Argentina in the Middle Miocene, and in North America as early as the Lower Eocene. The presence of cracids in the Miocene in South America (if proved) is not in conflict with the view expressed in this paper that the *modern* cracid genera originated in North America.

in particular with *Penelope pipile*, in proportions, I do not see the necessity of such an action, at least until more fossil material has been accumulated.

The erection of a new genus, *Palaeonossax*, from only the distal end of a right humerus, and after comparison with only three modern genera, *Crax*, *Penelope*, and *Ortalis* (Wetmore, 1956), appears somewhat questionable, especially since the fragment is without doubt quite similar to the same part in *Ortalis*. The same could be said about *Boreortalis* (Brodkorb, 1954), although the describer was careful to compare the bone (a tibiotarsus) with *Penelopina*, noticing its resemblance to that genus as well as to *Ortalis*.

The three remaining fossil cracids were originally described as *Ortalis*, but Wetmore (1951) expressed some doubts about their generic allocation. There is furthermore the possibility that *Cyrtonyx tedfordi* of the Barstow Formation (Upper Miocene of California) should be removed from the Odontophorinae and put into the Cracidae (Holman, 1961: 194–195). The only South American fossils are fragments of *Crax* and *Penelope* from cave deposits from the Pleistocene of Brazil (Wetmore, 1956).

Although the fossil record of the Cracidae is poor, it is better than in many other groups of birds, and permits the following comments to be made:

1) The family Cracidae occurred in North America from the Middle Eocene until at least the Pliocene.

2) Even the earliest fossils are not very different from modern ones. *Gallinuloides* is a small cracid, rather generalized, but, judging from the limb proportions, it was certainly quite arboreal, at least as much as some of the most arboreal modern species, like the *Penelope pipile* species-group. The same was true also for *Procrax* (Tordoff and Macdonald, 1957). The family must have been arboreal for a long time, and the acquisition of terrestrial habits (in *Crax*, *Penelopina*, and *Oreophasis*) appeared secondarily and perhaps independently in several groups of cracids.

3) Whether *Ortalis tantala*, *O. pollicaris*, and *O. phengites* really belong in *Ortalis* or not is rather unimportant. What is important is that *Ortalis*-like cracids have existed since at least the Upper Oligocene—since *Palaeonossax* is closely related to *Ortalis*. The fact that *Boreortalis* has characters reminding one of both *Ortalis* and *Penelopina* may indicate the approximate time of the separation and radiation from their common stock.

4) As several authors have already pointed out, the fossil record definitely indicates that the family underwent an extensive radiation in the Tertiary of North America.

TERTIARY HISTORY OF THE CRACIDAE

During the early Tertiary, ecological conditions in the west-central United States were quite favorable for cracids, offering them suitably forested areas. In the Middle Eocene, subtropical climate in the lowlands, more temperate in the adjacent uplands, occurred at least as far north as Wyoming (Chaney, 1947), where *Gallinuloides* was found.

From the Oligocene on, the climate in this central area of the United States became progressively more temperate, and the flora took on a slightly more xerophytic aspect in the uplands, where patches of savanna probably alternated with thicker woods (Axelrod, 1958). There was still dense gallery forest along the waterways. These conditions prevailed in central United States until at least the late Miocene (MacGinitie, 1962). Climate and vegetation must not have been much different from what is found now in southern South America (southern Brazil, Paraguay, and Uruguay). Later, up to the Pliocene, there was favorable cracid habitat in North America as far north as the Dakotas, but at this time this habitat might have been restricted to the watercourses.

That favorable cracid habitat, even if restricted in area, was occupied by cracids is shown without a doubt by the fossils found in Nebraska and South Dakota from the Oligocene to the Pliocene. But it should be kept in mind that it is unlikely that this region of North America ever was the main center of cracid distribution. In other words, suitable habitat in the Dakotas and in Nebraska (and in other central states) constituted probably the northern limit of cracid distribution then, just as suitable habitat in southern Brazil, Paraguay, and Uruguay is the southernmost limit now. Where the main center was is of course impossible to determine in the absence of an adequate fossil record, but it should not be unreasonable to consider the southern United States and México as a likely place, in view of the extensive areas of humid forests there during the early Tertiary (Chaney, 1947).

It might be that the rapidly increasing aridity in North America after the mid-Pliocene, together with the closing of the Panamá water gap, may have furthered the chances for cracid emigration into South America. Tordoff and Macdonald (1957) suggested that "the retreat southward . . . may have been hastened or brought about by competition with contemporaneous species of the Tetraonidae and, perhaps, Odontophorinae."

The present distribution of the Cracidae in the Americas and their degree of morphological divergence and of isolation suggests that most species inhabiting South America are of recent origin, probably post-Pliocene, and possibly as recent as mid-Pleistocene.

VARIATION AND SPECIATION IN THE GENERA PENELOPE AND CRAX

The preceding sections reviewed the significance of structural characters, hybridization, and the fossil record for the Cracidae as a whole, providing thus the necessary background for an analysis of species and potential species in each genus. I have chosen to discuss these topics for the genera *Penelope* and *Crax*.

Penelope

On the basis of color pattern, size, proportions, and wattle structure, the species of *Penelope* can be grouped into four species-groups, one of which constitutes the former genus *Pipile*.

1) *Pipile* Species-group

This contains two polytypic species, *pipile* and *cumanensis* (see Fig. 10). The distribution of *P. pipile* is made up of three isolated, morphologically very similar populations: *pipile* occurs only on Trinidad, where it is probably scarce (Herklots, 1961); *cujubi* along the south bank of the Amazon; and *jacutinga* in wet forests of southeastern Brazil, and gallery forests of Argentina (Misiones) and Paraguay. The two subspecies of *cumanensis* can be distinguished at once from any of *pipile* by the green gloss of their back (purplish in *pipile*). However, the two species are much alike in other characters, the form *cujubi* possessing characters of both. Indeed, *cujubi* has naked lores and chin and a white forehead like *P. cumanensis*, and the same purple gloss and crown color as *P. pipile jacutinga*.

Penelope pipile jacutinga is sympatric in Paraguay with *P. cumanensis nattereri* (see Laubmann, 1939: 128), so the two forms should be considered specifically distinct. An alternative possibility would be that the Paraguay population is polymorphic, and that there is only one species. Since the two forms differ in several characters it would seem correct to infer that two species are involved.

The *pipile* species-group may represent the descendants of a rather old stock more strictly adapted to arboreal life in humid forests than other members of *Penelope*. The separation into the two modern species might be recent, but so little is as yet known of their ecological requirements in the area of overlap and elsewhere that it is not possible to determine what the isolating factors

Fig. 10.   Distribution of the *Penelope pipile* species-group.

might have been. It seems that the range of *P. pipile* might have been reduced by the increase in less favorable habitat in various parts of Brazil (in particular the more xero-phytic uplands). *P. cumanensis*, on the other hand, might be a more aggressive species, which spread into areas previously occupied by *pipile*, or which eliminated *pipile* by competition.

2) *Jacucaca* Species-group

The three forms (*jacucaca*, *pileata*, *ochro-gaster*) of this group are so similar that I feel confident that they are members of one

polytypic species; there does not appear to be any overlap in their ranges. They have a rather restricted distribution in central and eastern Brazil, only one form (*pileata*) being actually spatially isolated from the others (Fig. 11).

The affinities of *jacucaca* with the *pipile* species-group are obvious, although their proportions are somewhat different, the tarsus being proportionately shorter in *pipile* and *cumanensis*. In my opinion the *jacucaca* species-group, because of its resemblance to both the *pipile* group and the *purpurascens* group, links all these birds and suggests that they are all derived from a common ancestral stock.

3) *Purpurascens* Species-group

The several recognized forms that compose this group have been variously considered as four species (*purpurascens, jacquaçu, granti,* and *obscura*) by Hellmayr and Conover (1942), or only two species (*purpurascens* and *obscura*) by Peters (1934). Although neither classification is really satisfactory, Hellmayr and Conover's is somewhat better in view of the incorrect merging of *granti* with *marail*, as was done by Peters. For convenience, Hellmayr and Conover's nomenclature has been adopted in the map (Fig. 12), although I only recognize one species in this complex, as explained below.

Difficulties experienced by previous authors working with these forms were due in part to their failure to recognize the great amount of individual variation in any one population. Blake (1955), taking this fact into account, concluded correctly that *purpurascens* and *jacquaçu* are conspecific (this had already been suggested by Dugand, 1952). In British Guiana, southern Venezuela, and northern Brazil, the forms *granti* and *orienticola* are fully intergrading, as was shown by Conover and Phelps (1946). The same authors pointed out that no intergradation was known to take place between *jacquaçu* and *granti-orienticola*, and maintained the two groups as separate

Fig. 11. Distribution of the *Penelope jacucaca* species-group.

species. However, lack of intergradation seems to be only a reflection of the lack of adequate collecting in extreme southern Colombia. Indeed, Dugand (1952) mentioned the intermediate characters of three specimens from the Río Apaporis, southeastern Colombia, which show features of both *orienticola* and *jacquaçu*.

Hellmayr and Conover (1942) and later Blake (1955) maintained that the differences in proportions between the Bolivian forms *jacquaçu speciosa* and *obscura bridgesi* are such as to warrant specific distinctness of *jacquaçu* and *obscura*. After computing several ratios (wing/tail, tarsus/wing, tarsus/tail) in 8 specimens of *jacquaçu jacquaçu*, 6 of *jacquaçu speciosa*, and 11 of *obscura bridgesi* I can only conclude that these differences are no more than clinal, with perhaps a sharper step between *speciosa* and *bridgesi*.

The present distributional gap between the montane *bridgesi* in northwestern Argentina and the riverine *obscura* in Paraguay, Uruguay, and Argentina (Misiones) appears to be a consequence of the recent

Fig. 12.   Distribution of the *Penelope purpurascens* species-group.

□ PURPURASCENS
○ JACQUAÇU
● GRANTI
▲ OBSCURA

increase of more xerophytic vegetation un-favorable to these birds. In view of the lack of marked differentiation between *bridgesi* and *obscura* it is likely that gene flow was continuous between them, and that the present distribution of *bridgesi* represents a secondary dispersal toward the north that took place shortly after the estab-lishment of the drier belt in Paraguay and Argentina.

From the above evidence it seems to me that the whole *purpurascens-jacquaçu-granti-obscura* complex should be treated as one species. As far as the material I have examined permits one to judge, variation in this complex is mostly clinal, and therefore it becomes rather difficult (and in some cases certainly unnecessary) to assign names to some populations. The birds of British Guiana, southern Venezuela, and northern

Fig. 13.   Distribution of *Penelope argyrotis*.

Fig. 14.   Distribution of *Penelope superciliaris*.

Brazil ("*granti-orienticola*"), and of southern Bolivia, Argentina, Paraguay, Uruguay, and southern Brazil ("*bridgesi-obscura-bronzina*") are slightly different in color and size, respectively, from the birds of Colombia, Ecuador, Perú, western Brazil, and northern Bolivia ("*purpurascens-jac-quaçu*"). These peripheral populations may have been isolated for some time as suggested by the probable stepped clines. Of course, only examination of more extensive material will permit a definite conclusion about the variation within this complex, and its interpretation.

The overall pattern of variation and of distribution of populations of the *purpurascens* species-group suggests that the pro-*purpurascens* ancestor probably reached South America from the north in the Pleistocene and, once there, dispersed rapidly into all suitable habitats. The total range of the group corresponds closely to the extent of dense humid forest (rain forest, montane forest, gallery forest along watercourses) in Central and South America.

4) *Montagnii* Species-group

I recognize four species in this group: *argyrotis, superciliaris, montagnii,* and *marail*. The specific limits are certainly easier to draw in this group than in the *purpurascens* group because some morphological characters are invariably present in a given

species, and totally lacking in the others. The species in this group are generally smaller than the populations of *purpurascens*. *P. argyrotis* is distinguished from all other forms of the *montagnii* group by the cinnamon color of the tip of the rectrices. It contains six named subspecies, morphologically quite similar. The most distinct is *columbiana* from the Sierra de Santa Marta in northern Colombia, and not, as one would expect, the isolated *barbata* of southern Ecuador and northern Perú (Fig. 13).

Brown edges of the secondary wing coverts and innermost secondaries are distinctive of *P. superciliaris,* much more so than the silvery supercilium, which is quite variable; some subspecies of *P. montagnii,* in particular *plumosa* and *sclateri* of Perú and Bolivia, have a stripe reminiscent of the one in *superciliaris.* This species comprises four subspecies showing clinal color variation, occurring in Brazil over a vast area, west to the Rio Purús, south to Rio Grande do Sul, and across into Argentina (Misiones) and Paraguay (Fig. 14).

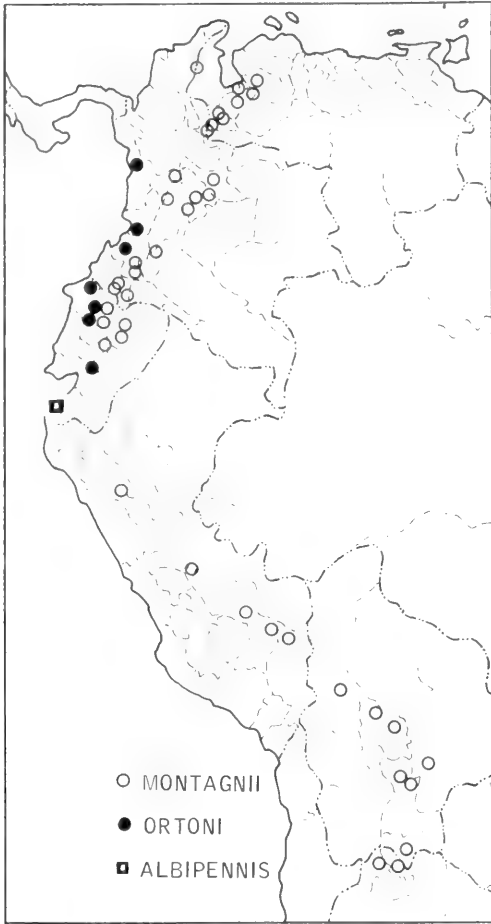The third species contains *P. montagnii,* with 7 described subspecies from northern

Fig. 15.   Distribution of *Penelope montagnii*. For discussion of *ortoni* and *albipennis* see text.

Colombia and Venezuela to Argentina (Fig. 15). Olrog (1960) rightly showed that *dabbenei* of southern Bolivia and northern Argentina is only a subspecies of *montagnii* and not a distinct species, as formerly believed (Hellmayr and Conover, 1942). All variation in *montagnii* seems to be clinal but this should be studied with more material than I have seen in order to check whether the variation between *brooki*, *plumosa*, *marcapatensis*, and *sclateri*, and possibly also *dabbenei*, represents one or more stepped clines.

There is the problem of the allocation of

three other forms: *marail*, *ortoni*, and *albipennis*. *P. marail* is widely distributed in Brazil north of the Amazon, in the Guianas, and a small area in Venezuela (Fig. 16). For a long time this form was confused with *P. purpurascens granti*, for example by Peters (1934), because the two are rather similar in the color of the upper parts, glossed with metallic green. In other color characters and proportions, however, *marail* is distinct from *granti*. It is much closer to the *montagnii* group, even though its tail is proportionately shorter than that of the various species of the *montagnii* group. In view of these differences, and pending further evidence, I think it best to treat *marail* as a species. *Penelope ortoni* is certainly closely related to *P. montagnii atrogularis* (color of upper parts and crown), and *montagnii plumosa* (color of under parts), and should be included in *montagnii*, of which it is a representative in the lowlands of western Colombia and western Ecuador (Fig. 15). *Penelope albipennis* was described by Taczanowski (1877) on the basis of a single specimen collected by Stolzmann near Tumbez in northwestern Perú, and on the assertion of Stolzmann that all the *Penelope* which he saw near Tumbez (Santa Lucia) had white primaries. There are now two specimens extant, the type in Warsaw and a mounted bird in the Museo "Javier
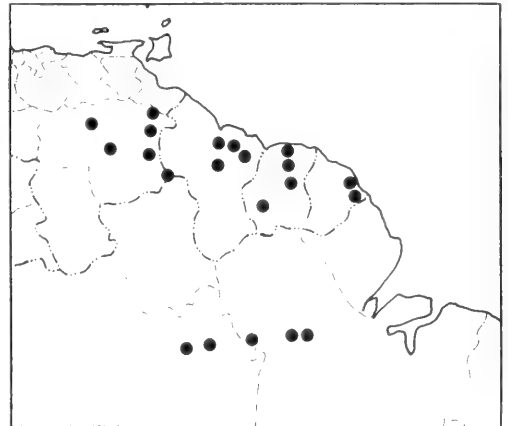

Fig. 16.   Distribution of *Penelope marail*.

Prado" in Lima (Ridoutt, 1939). In this form, the eight outer primaries are white with the base and the tip dark. This is reminiscent of partial albinism found in a population of *P. montagnii ortoni* in Colombia. Six specimens in the Academy of Natural Sciences of Philadelphia collected by A. de Buey in the Chocó present various amounts of whitish-isabelline in several parts of the body: neck, breast, back, wing coverts, primaries, secondaries, rectrices, and the head (crown feathers). It is noteworthy that two other birds collected at the same locality by de Buey are similar to normal specimens of *ortoni*. This suggests that some populations of *ortoni* have a tendency for developing whitish areas in the otherwise dark plumage. I strongly suspect that the so-called *albipennis* is nothing else than a similar variant of *ortoni*.

Sympatry between the species of the *montagnii* group occurs only in a few narrow zones: in the Perijá Mountains (Colombia-Venezuela boundary), and in southwestern Venezuela, between *P. montagnii* and *P. argyrotis*.

The range of most species of the *montagnii* group does not overlap with *P. purpurascens*, but where two occur in the same locality, as in Venezuela, they occupy different niches: *P. purpurascens* lives in the treetops and *argyrotis* in the median and lower strata (Schäfer, 1953). The fact that the voice and tracheal structure are different, at least in *purpurascens* (high-pitched voice, simple trachea in both sexes) and *argyrotis* (deeper, more raucous voice, tracheal loop present in the male at least), also suggests that these two groups are not so closely related, in spite of the similarities in plumage pattern. The fact that the *montagnii* species-group is fractioned into more species and subspecies may mean that the group is older, but may also indicate that isolating factors are more active in mountain areas than in lowland ones. On the other hand, the fact that there are more forms in the northern part of the range of the *montagnii* species-group may not indi-

cate a place of origin but simply that there is more favorable habitat there, and that the birds took full advantage of it.

I think that the pro-*montagnii* ancestor was already more strictly adapted to mountain conditions at the time it invaded South America, and that it did so earlier, but not much earlier, than the pro-*purpurascens* ancestor. The possibility of former isolation at the periphery of the range (*marail*) and in the south (southern forms of *montagnii*) suggests that the same factors have been operating in the *purpurascens* group.

Crax

This genus contains about 13 forms, easily separable into two species-groups. One of them (*rubra* species-group) is the former genus *Crax* (*sensu stricto*), the other (*mitu* species-group) contains the former genera *Mitu*, *Pauxi*, and *Nothocrax*.

1) *Rubra* Species-group

The eight forms comprising this group are very closely related, essentially allopatric, the only known area of sympatry being a narrow one between *rubra* and *alberti* in the Sinú Valley of Colombia (Blake, 1955). The area covered by these eight forms is considerable, and corresponds almost to the present extension of dense humid forest in Central and South America (Fig. 17). In marginal areas, or in regions where the forests have been destroyed by man in recent times, the birds still subsist in islands of forest. This is the situation for *C. blumenbachii*, an apparently rare species in eastern Brazil (Stresemann, 1954; Greenway, 1958), where its habitat has been reduced enormously in recent years.

In spite of some variation, all forms of the *rubra* species-group are quite similar in color pattern, the males being black except for a patch of white on the lower belly, the females being barred with white above, and brown underneath (the exceptions are the females of *C. alector*, which are almost similar to the males, and the females of *C. daubentoni*, which do not have any brown,
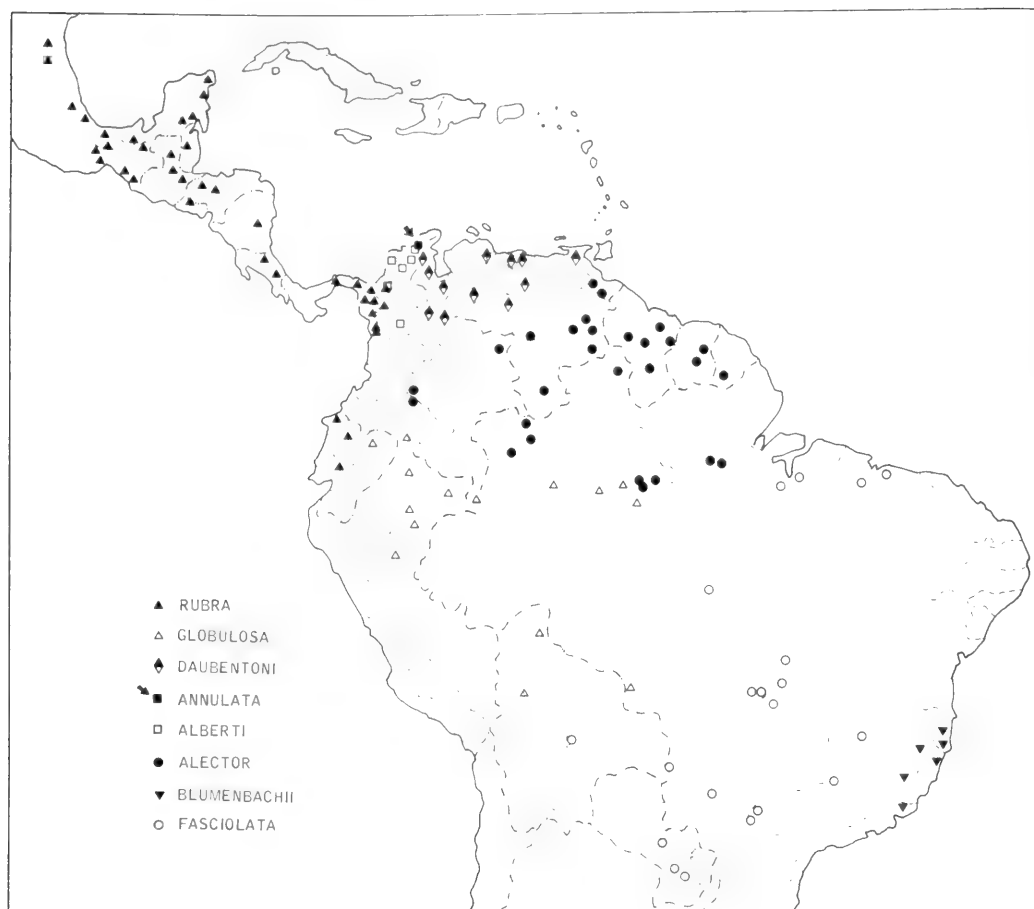
Fig. 17. Distribution of the *Crax rubra* species-group.

only white barrings in the black plumage). Both sexes of all forms have a crest of long, always erected, and curly feathers. All forms except *blumenbachii* have an area of bare skin on the face, sometimes restricted to a small zone around the eye (*rubra*), sometimes much more extensive (*fasciolata*). Most forms have a frontal protuberance, sometimes quite big (*rubra*), usually bright yellow. Some forms have in addition to the frontal knob a pair of wattles at the base of the lower mandibles, that have the same color as the knob. It seems that forms that have no frontal protuberance have a bigger naked area on the face than the others. There is much variation in

both wattles and knob, however, especially in *C. globulosa*; also *blumenbachii* does not have any area of bare skin on the face, nor does it have wattles or knob.

Another sort of variation is exhibited by the females. In *rubra* in particular, which is certainly the best-known species, at least two color phases are described (Ridgway and Friedmann, 1946). The situation requires much more study on the other forms before one can be certain of the range of variation in the female plumage. Such an investigation may be interesting in view of behavioral differences between birds having different looking females. Thus the sexually dimorphic *C. rubra* is monogamic

Fig. 18.   Distribution of the *Crax mitu* superspecies (mitu-tomentosa-salvini).

and territorial, while the (almost) non-dimorphic *C. alector* seems to be polygamous, and *C. daubentoni*, where the female is much masculinized in aspect, seems to occupy an intermediate position, in which polygamy occurs but may not be absolute.
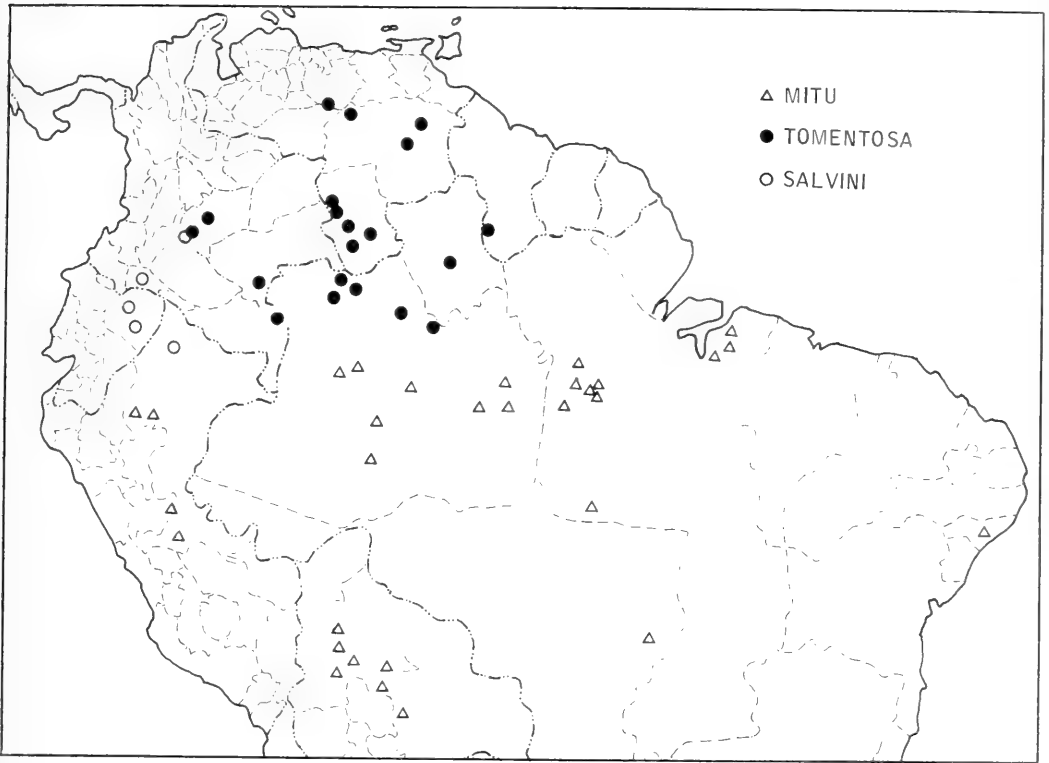
For the present I consider it best to treat the various forms as specifically distinct. *Crax rubra* and *C. globulosa* look more alike than other forms, so I have included them in a superspecies. Similarly, the three forms *alberti*, *annulata*, and *daubentoni* are closer to each other than to any other form, and I include them, too, in a superspecies. The status of *annulata* requires further study, however, and its position as a species must be considered provisional, pending further evidence. It is possible that a detailed study of variation in this species-group will show all forms to be members of a single superspecies.

The genetic compatibility of various species crossed in captivity indicates that speciation is in an early stage. The rapid development of structures such as wattles, frontal protuberance, and areas of naked skin on the face suggests a rapid and recent diversification in isolated, allopatric populations, and should not be taken as an index of the degree of differentiation of populations. Rather, uniformity in tracheal structure and voice, in color pattern, in habitat, and in diet points to the *rubra* species-group as a very young one. The distribution of the group suggests a rapid dispersal from a pro-*rubra* ancestor that was able to colonize widely in South America in the Pleistocene. This ancestral population may have been quickly broken down into several subpopulations isolated from each other by some ecological barriers and resulting in the pattern observable now.
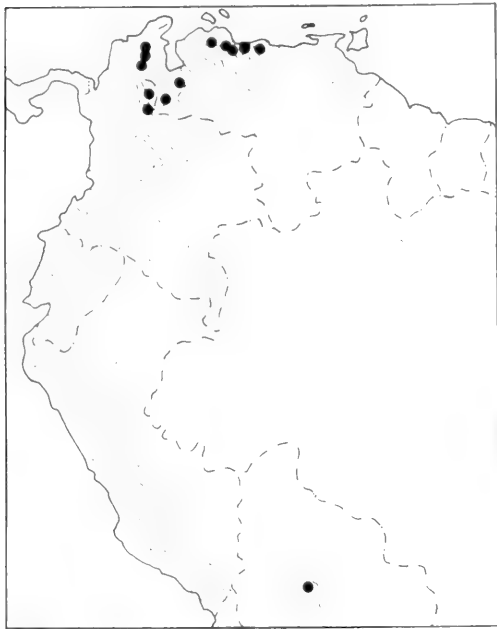
Fig. 19.   Distribution of *Crax pauxi*.

2) *Mitu* Species-group

The five forms of this group are also very closely related to each other and obviously derive from a common stock which in turn is common with the ancestral stock of the *rubra* species-group. The differentiation is so slight that the separation into the two species-groups must have been recent.

Here again, allopatry is the rule, especially in the *mitu* superspecies (see Figs. 18 and 19). As far as I can tell, the only area of sympatry is in the southern Sierra de la Macarena, Colombia, where *Crax salvini* and *C. tomentosa* were taken within a few days of each other (Olivares, 1962). *C. urumutum* (Fig. 20) broadly overlaps the ranges of *mitu* in upper Amazonian Brazil and Perú, *salvini* in Ecuador, and *tomentosa* in southwestern Colombia and western Venezuela. These five forms show a great uniformity in plumage pattern in both sexes, and in tracheal structure. Variation is found in the absence or presence of elongated crest feathers, in the presence or absence of a casque, and in the color of

the lower belly. The females are always similar to the males in plumage color, but they are somewhat smaller. A brown color phase in *Crax pauxi* was first described by Sclater and Salvin (1870), and studied by Phelps and Phelps (1962). Four birds out of 64 in European, American, and Venezuelan museums showed this rufous coloration. Two of them were unsexed, and the other two were females. This plumage does not seem to be juvenile since an unsexed brown bird kept in the Maracaibo Zoo for years never changed color.

There is little doubt that three of the species, *tomentosa*, *mitu*, and *salvini*, are closer to each other than to the other two. Whether they should be considered a single species is debatable in view of the possible sympatry of two of them in the Sierra de la Macarena. For this reason, I have treated them as a superspecies. *Crax pauxi* differs from the preceding three in its enormous casque and should be regarded as a distinct species exhibiting some variation in the dimensions of the casque and the shape of the crest feathers. The disjunction (Fig. 19) may be less striking than it seems, because it would not be surprising to discover intermediate populations in Ecuador or Perú. This disjunction reminds one of that of *Tinamus osgoodi*, allied to *T. tao*, which has been found in the Río Aguas Claras,
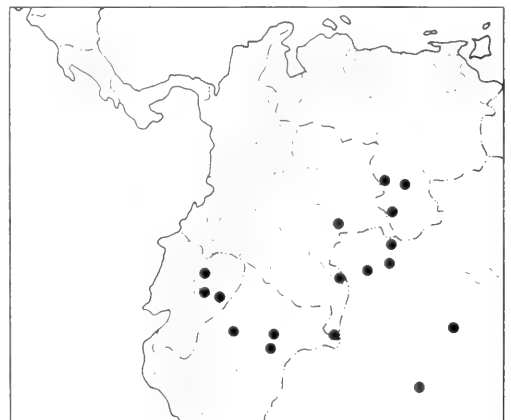
Fig. 20   Distribution of *Crax urumutum*.
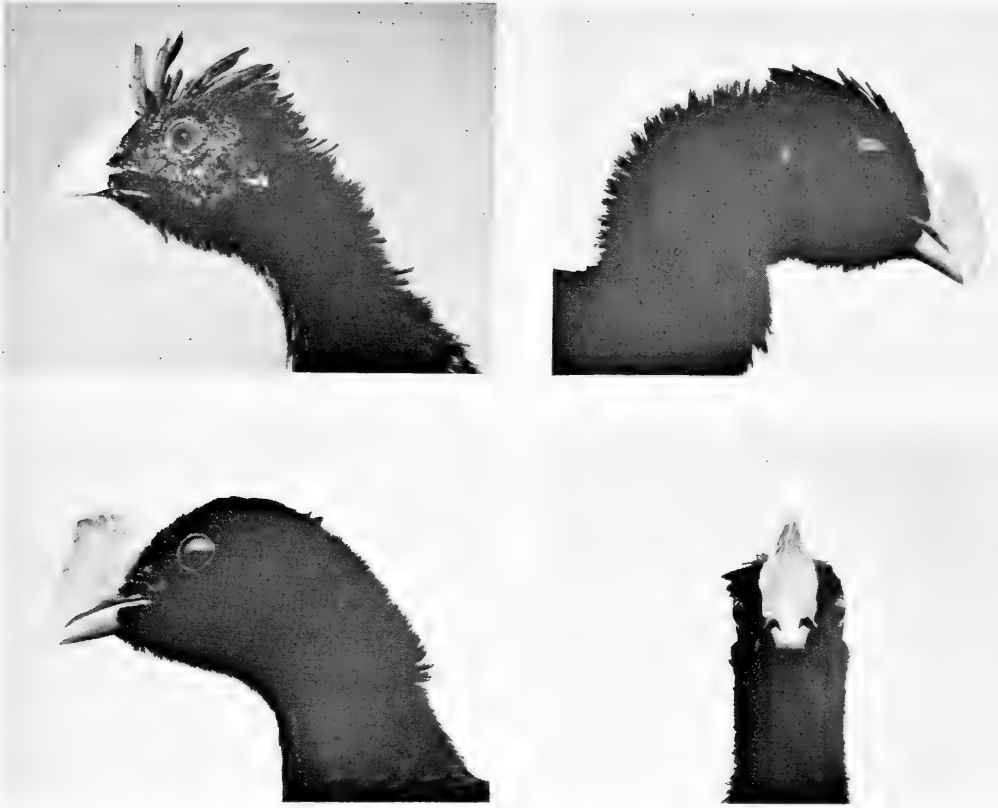
Fig. 21. Variation in the size and shape of the casque of *Crax mitu.* Upper left: young bird (age 6½ months). Upper right: adult female. Lower, left and right: adult male. (Photographs courtesy John A. Griswold and Zoological Society of Philadelphia.)

Huila, Colombia, and in the Marcapata Valley, Cuzco, Perú. In either case it is difficult to account for the disjunctions, but one may surmise that among such sedentary and territorial birds as *Crax pauxi* and *Tinamus osgoodi* extinction can occur in continental forest areas as readily as in island areas.

DISCUSSION

From the analysis of variation and distribution, it can be seen that *Penelope* and *Crax* show the same basic patterns of speciation. In both these genera, the members of a species-group are mostly allopatric representatives of one or more superspecies.

These representatives, or species, are, for the main part, in a relatively early stage of speciation. Whether they should be called species or subspecies is not always easy since the criterion of interbreeding in nature can not be applied as it could with sympatric species. In the case of *Crax* in particular, morphological divergence might lead to the belief that the various forms have reached levels of speciation beyond those actually attained. The evidence of hybridization in captivity, but not in the wild, is here a far better criterion than morphology alone since it indicates that an intermediate stage in the development of the isolating mechanism has been reached (i.e., there is little genetic isolation).

This general pattern of allopatric species most likely ethologically isolated in the few narrow areas of overlap, suggests that the ancestral stocks of the species-groups in both *Penelope* and *Crax* reached, or have been in South America only since the Pleistocene. Although the speciation pattern of *Ortalis* has not been described, a preliminary investigation revealed a situation similar to that of *Penelope* and *Crax*. This same pattern of radiation in the three genera that comprise the majority (87%) of the species of the Cracidae strongly suggests that a nearly simultaneous dispersal preceded differentiation in allopatric populations (probably isolated by slight ecological differences) during the Pleistocene. The fact that each genus has such a broad distribution in all favorable habitats of Central and South America, together with a consideration of the stage of speciation in which they occur, suggest further that the habitats were empty at the time of dispersal and that the ancestral forms probably came from the north outside South America.

The four other genera that do not exactly correspond to the patterns of *Ortalis, Penelope,* or *Crax* are: 1) *Oreophasis*, restricted to the high mountains of southern México and Guatemala, 2) *Penelopina* in mountains from southern México to Nicaragua, 3) *Chamaepetes*, with one species (*unicolor*) in the mountains of Costa Rica and Panamá, and the other (*goudotii*) in the Andes from Colombia to Perú, and 4) *Aburria* in the Andes from Colombia to Perú. These four genera appear to be descendants of a stock that underwent an early radiation in North America. Two of them, *Chamaepetes* and *Aburria*, have conserved some of the supposed primitive characters of the ancestral form: very arboreal habits, ecological association with humid forests, lack of patterned plumage, and, in the case of *Chamaepetes*, absence of head or neck ornaments or areas of naked skin. *Penelopina* shows what is certainly secondarily acquired sexual dimorphism, complete polygamy, and partially terrestrial

habits (nest regularly on the ground). In appearance, *Oreophasis* is the most unique cracid and also exhibits some secondary specialization, such as ground-nesting habits.

At some point during the late phases of this North American radiation the forms that were going to invade South America and give rise to the modern species of *Penelope* and *Crax* evolved from a stem closely related to *Penelopina, Chamaepetes,* and *Aburria*, while *Ortalis* had already undergone radiation when some stock reached South America.

SUMMARY

1) The majority of species (87%) of Cracidae belong in the three genera *Ortalis, Penelope,* and *Crax*. The former genus *Pipile* has been included in *Penelope*, and the former genera *Nothocrax, Mitu,* and *Pauxi* synonymized with *Crax*. Among the genera retained, *Chamaepetes* and *Aburria* were found to be very close to *Penelope, Penelopina* to be intermediate between *Ortalis* and *Penelope*, while *Oreophasis* is somewhat aberrant.

2) Variation and function of casque, crest feathers, wattles, attenuated primaries, tracheal loop, and color pattern are discussed. It is shown that structures such as casque, wattles, and areas of naked skin on the throat are probably of use as species-specific recognition marks, and hence should not be utilized as taxonomic characters for distinguishing genera. In *Ortalis* and *Crax*, plumage pattern, tracheal morphology, and voice are very uniform. In *Penelope*, color pattern and tracheal structure are variable, but all species have a wattle (dewlap or area of naked skin on the throat) and erectile crest feathers.

3) No hybrids have been found in nature, but hybridization in captivity is not rare. In only one series of experiments was hybridization attempted by the aviculturist beyond the F_1 generation. In this case, crosses between *Crax mitu* and *Crax alberti* produced completely interfertile F_2 offspring. From this evidence it seems probable that in

nature isolating mechanisms are ethological (as well as ecological) in the narrow zones of sympatry.

4) Seven fossil cracids show that the family occurred in North America from the Eocene to the Pliocene. This record indicates that *Ortalis*-like cracids were present in North America since the Upper Oligocene. The only fossil remains found in South America are of *Crax* and *Penelope* in Pleistocene Brazilian cave deposits. It seems probable that the Cracidae originated in the warmer parts of early Tertiary North America and radiated in this region long before they reached South America.

5) An analysis of speciation in *Penelope* and *Crax* reveals that in each genus the "species" are in an intermediate stage of the speciation process, i.e., the "species" are allopatric members of superspecies. In no species-group is there any broad sympatry between related species. It is postulated that the three main genera of Cracidae, *Ortalis, Penelope*, and *Crax*, have colonized South America in the Pleistocene, by means of ancestral forms that originally came from North America.

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The Distribution of the Oceanic Fish
Brama brama

by GILES W. MEAD and RICHARD L. HAEDRICH

Museum of Comparative Zoology, Harvard University; and
Woods Hole Oceanographic Institution

THE DISTRIBUTION OF THE OCEANIC FISH *BRAMA BRAMA*

GILES W. MEAD AND RICHARD L. HAEDRICH

INTRODUCTION

This study is chiefly an analysis of the distribution and seasonal migration of *Brama brama* and, to a lesser extent, of *B. japonica*. These are relatively large mesopelagic fishes of temperate and subartic waters, the habits of which are largely unknown except for the published and original data summarized here. The genus also includes several tropical species, which will not be considered. *Brama* as a whole will be treated in a later paper together with *Taractes, Taractichthys, Eumegistus, Pteraclis,* and *Pterycombus*, the six genera forming the family Bramidae.

Although *Brama brama* occurs in the Southern Hemisphere, our study is restricted to the North Atlantic population. Data on adult distribution has been taken from many published records, and from the commercial fishery statistics of Spain, where the species is landed in noticeable quantity. The monthly occurrence or abundance of these adults has been correlated with the approximate position of the 10°C (50°F) isotherm; and the 10°C isothere virtually limits the northernmost occurrence, as shown by all records combined. Spawning area has been estimated from an analysis of larval distribution, an investigation based largely on the plankton collections of the "Dana" expeditions. Spawning, as reflected by the distribution of the larvae, occurs in waters warmer than about 20°C (68°F).

During recent years an interest in the distribution, abundance, and possible commercial importance of the Pacific *Brama japon-ica* has developed. Exploratory gill-net surveys in the Gulf of Alaska were conducted by the U.S. Bureau of Commercial Fisheries, and these confirmed earlier reports that large numbers of *B. japonica* were seasonally and sporadically present there. A distributional study has been completed by Charles R. Hitz and Robert French of the U.S. Bureau of Fisheries, Seattle, Washington and is now in press. The information assembled by these authors and our Atlantic data were the subjects of personal discussions, and similarities between the habits of *Brama brama* and *B. japonica* suggested that features shown by one species might profitably be sought in the other. For example, *Brama brama* forms commercially significant concentrations in the eastern Atlantic, which we believe to be due to temperature-controlled seasonal migratory habits. Temperature may influence the movements and concentration of *B. japonica* in a similar way.

We will consider our Atlantic material first and follow with comparative notes on the Pacific species.

THE CENTER OF AVAILABILITY:
NORTHWESTERN SPAIN

Although bramids are landed as food fishes throughout the world, only off the west coast of the Iberian Peninsula does any species form the center of a fishery. In the principal area off northwestern Spain, there may be over a hundred vessels, each about 25 meters long, operating during the height
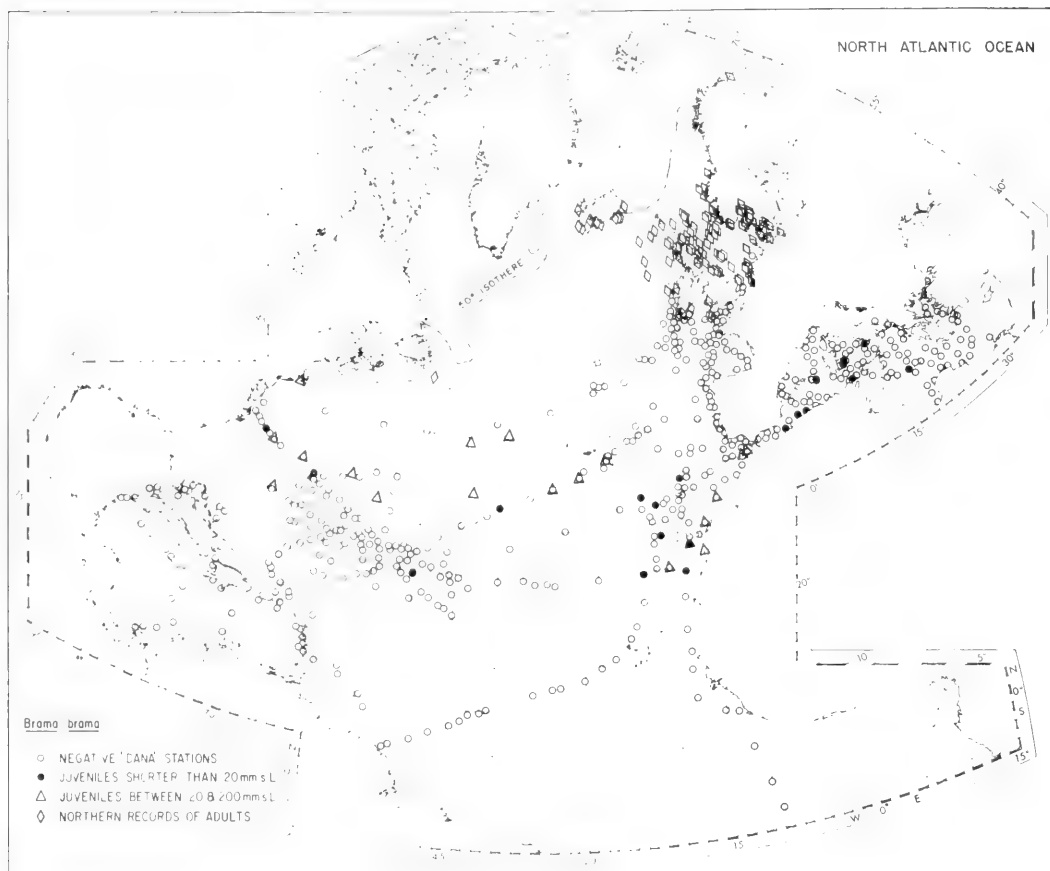
Figure 1. The distribution of the ''Dana'' stations in the North Atlantic and the known distribution of juvenile and adult *Brama brama*. The 50°F (10°C) isothere is taken from Hutchins and Scharff (1947).

of the season.[1] Each vessel sets and hauls about six miles of longline daily, a line similar to that universally used for tuna, but of lighter construction and with more numerous and smaller hooks. About seven thousand hooks comprise a set, which is made at about 50–60 fathoms (91–110 meters) in water over 250 fathoms (457 meters) deep. Catch rates frequently reach the

phenomenal values of 60 or 70 fish per hundred hooks. The fish can also be simply and plentifully caught by jigging. The principal fishery, a winter one, lies west of the Cies Islands, and contributes about two per cent to the total Spanish fishery landings (Table 1). During the summer the fishery is centered further north, the vessels operating from La Coruña and Santander; during the early winter it extends south to the offings of Portugal. Further discussion of the fishery and the commercial use of *Brama* here and elsewhere is deferred. It is sufficient to note that this high-seas mesopelagic species congregates off
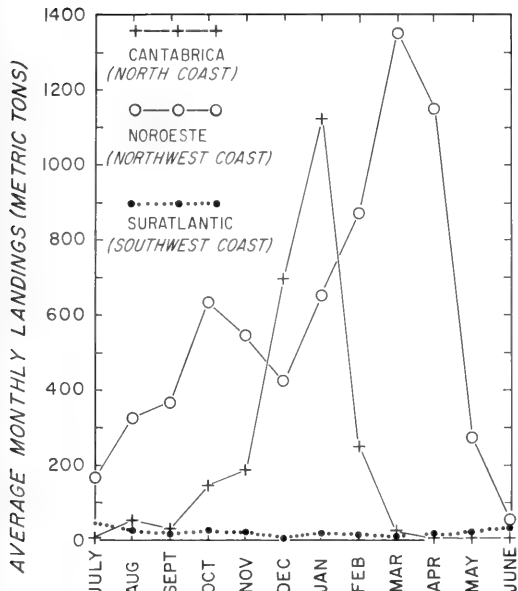
Figure 2. Ten-year average monthly landings of *Brama brama* in three Spanish coastal areas. Data from official Spanish fishery statistics (Anonymous, 1946).

Spain, and that landings data, using ten-year monthly means (Figure 2), show this congregation to be highly seasonal and at a maximum off the northwest coast during March and April when surface water temperatures are at their lowest. The gonads of the individuals which form this aggregation may be nearly mature, but the widespread occurrence of larvae in the eastern Atlantic and Mediterranean (Figure 1) south of, but not off, northwestern Spain suggests that the Spanish concentration is not a spawning aggregation. Other high-seas mesopelagic teleosts are caught incidentally on these winter longlines—fishes such as *Scombrolabrax*, *Gempylus*, *Lampris*, *Trachypterus*, and two additional bramids, *Pterycombus brama* and *Taractes asper* (= *T. raschi*).

DISTRIBUTION IN HIGHER LATITUDES

We consider next the distribution of adult *Brama* in waters which are of suitable temperature during a part of the year only. All known records except one are from the eastern Atlantic; the exception is a single cap-
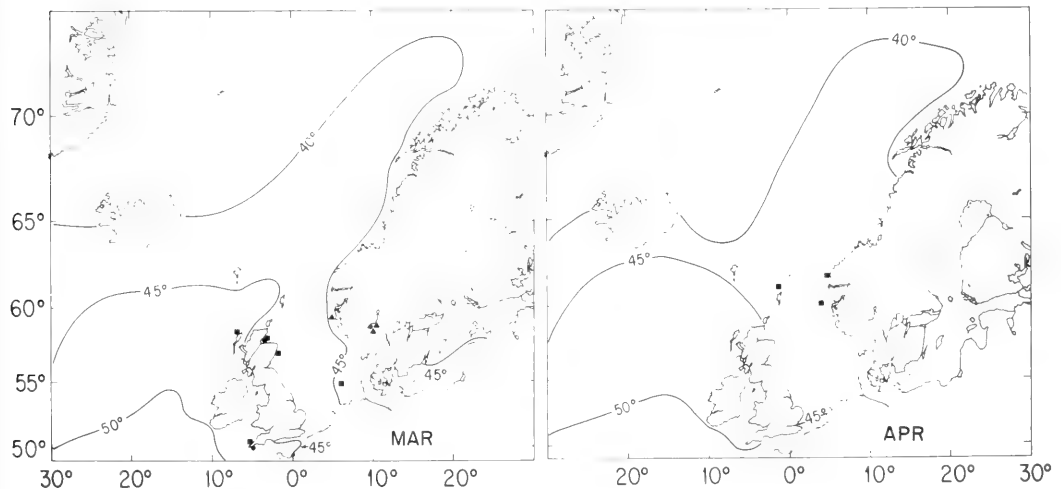
Figure 3A

Figure 3 A–F. Northern occurrence, by month, of adult *Brama brama*. ■ Live captures. ● Strandings. ▲ Circumstances unknown. Distributional data from Table 2; surface Isotherms (°F) from the U.S. Navy Hydrographic Office Atlas of Sea Surface Temperatures (Anonymous, 1948).
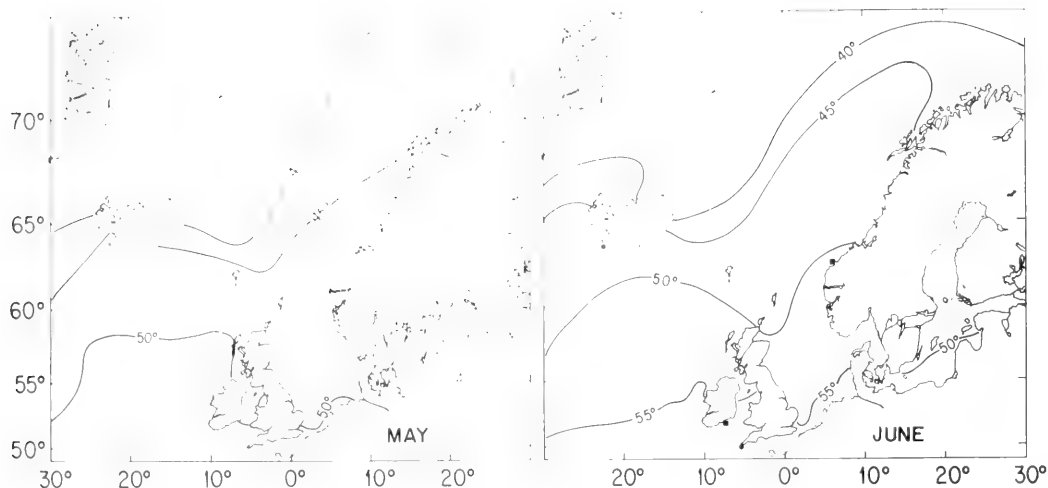
Figure 3B
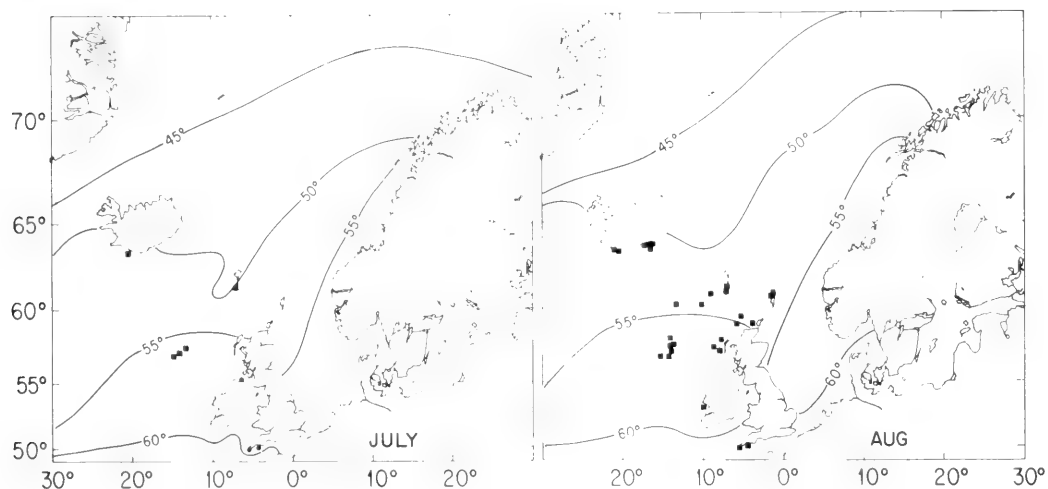
Figure 3C

ture made by a trawler on the Grand Banks off Newfoundland nearly a hundred years ago. In the eastern Atlantic, the species is exceedingly common in the Bay of Biscay. North of about 48°N the species is clearly a seasonal visitor and has been reported as such many times. These records, exclusive of some which seemed questionable and others which appeared to be duplicate accounts of the same specimen, are given in Table 2 and plotted in Figure 1. Also shown is the 50°F (10°C) isothere, north of which the surface waters are always colder than this (Hutchins and Scharff, 1947). This line appears to delimit the northward extent of all records except a single report from Murmansk.

Just as there are good and bad *Brama* years in the commercial fisheries of the south, there are years of numerous, and of few, reports to the north. During certain years, for example 1928 and 1949, the species
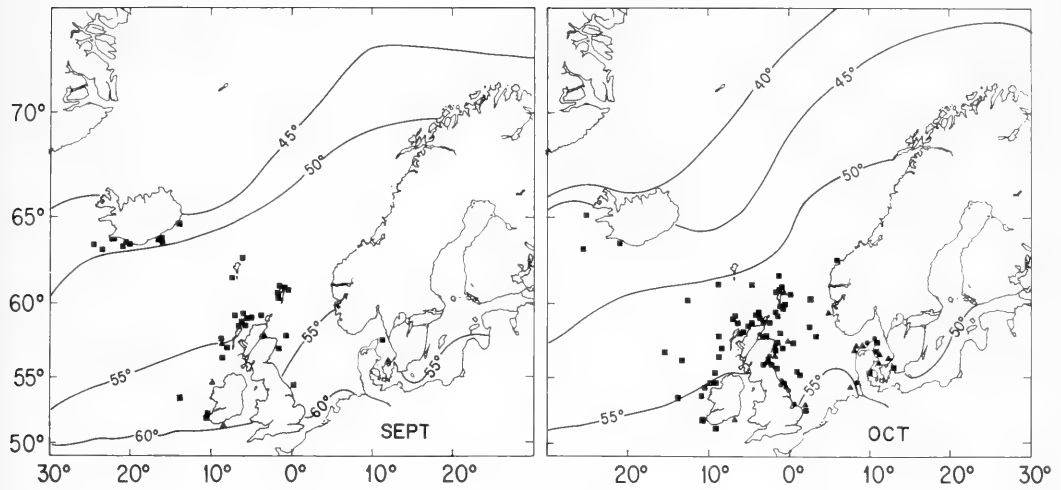
Figure 3D
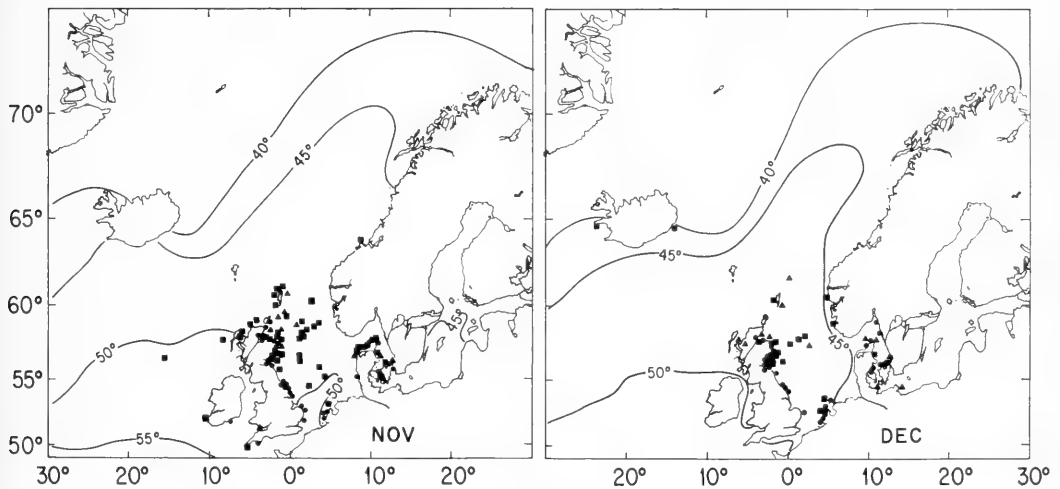
Figure 3E

was most abundant. Given these immense annual fluctuations, the unequal seasonal and geographic nature of fishing effort, of beachcombing, and of reporting, and the known climatic and related faunal changes which have taken place during the time span here considered, it may seem improper to dissect these data further, and we do so with a respect for these limitations.

The northern records (Table 2) are divided between live-captures and strandings, the latter term understood to include conditions of capture such as "nearly dead and awash in the surf" and "found floating dead at the surface." The reasons proposed for such strandings have been many and varied, e.g., the inability of a fish to determine the depth of the water, navigational difficulties similar to those which seem to beset the Cetacea from time to time, discomfort due to parasitism, etc. Such causes are unlikely, for strandiings are seasonal and occur most
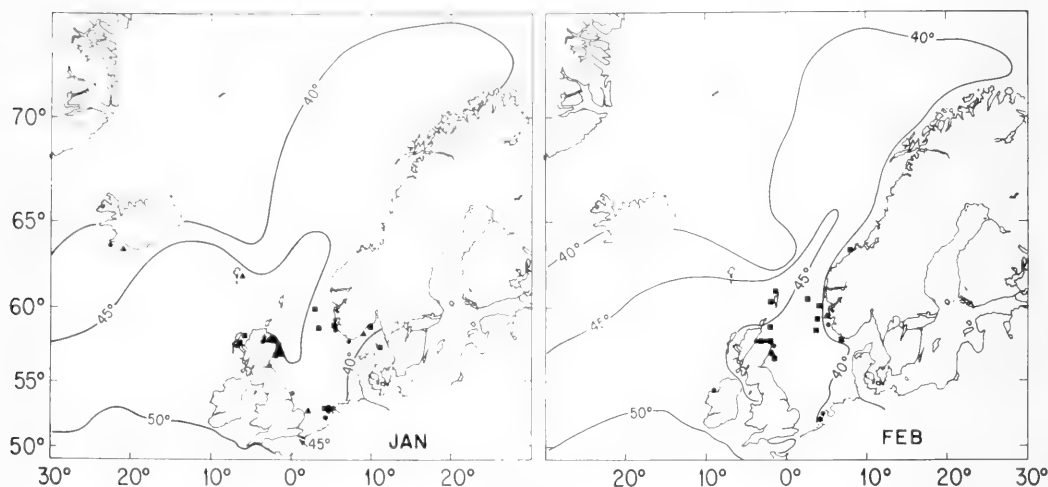
Figure 3F

frequently not in the southern waters in which *Brama* abounds, but in northern areas where it is less abundant. In accord with the conclusion of Kristensen (*in* Verwey, 1958: 544) and others, such strandings should be considered to be the result of low water temperatures aided, on occasion, by storms. These records were allocated to the calendar months, and the monthly records, together with the sea surface isotherms at 5°F intervals, were plotted on a series of charts (Figure 3).

During the winter and spring months the number of *Brama* apparently present in the north declines steadily. No specimen has ever been reported during May, and the reports for April and June are exceedingly few. This decrease probably represents the demise of the population which began its northward migration with the northward advance of warm surface water during April of the previous year. During June and July the surface waters in the north warm to 50–55°F (10–12.8°C) and higher, temperatures amenable to *Brama*, and following this warming come the fish. The August records are numerous and almost exclusively live-caught individuals. In September and October the critical isotherms begin their retreat southward. Reflecting this is the

reduction of *Brama* catches in Iceland and the increased concentration off Scotland and in the North Sea. During November and December the 50–55°F (10–12.8°C) water is no longer in the area and many *Brama* moving south but finding themselves in the North Sea rather than to the west of Scotland, are effectively trapped in this sea and the Danish Sound. Evidence of this distress is the high number of strandings relative to the number of live-caught individuals—evidence shown graphically in Figure 4.

TEMPERATURE AND DISTRIBUTION

A correlation between a physical and biological factor needs imply no direct causal relationship, but such correlations are nonetheless instructive. We must, however, enter an apology. We have used, in what may appear to be an indiscriminate fashion, temperature values both in degrees Fahrenheit and Centigrade. We would have preferred to use degrees Centigrade exclusively, and all original data have been so converted when necessary. But we have used two basic hydrographic works which present generalized temperature curves: Fuglister's paper (1954) on the average temperature at

a depth of 200 meters in the Atlantic, which summarizes over forty thousand observations and is presented in degrees Centigrade; and the "Atlas of Sea Surface Temperatures" (Anonymous, 1948), a summary of hundreds of thousands of temperature observations, which is presented in degrees Fahrenheit. Hutchins and Scharff (1947) compiled their most useful "isotheres" and "isocrymes" from this atlas; hence these curves too are in degrees Fahrenheit. Interpolation between curves would be unwise. We have chosen to use the curves closest to one another in temperature, identifying each, and hoping that the discrepancy so produced will not be too destructive to our description.

Although listed as a commercial species throughout the eastern North Atlantic, the magnitude of the catch of *Brama* reaches significant proportions only off the northwestern coasts of Spain and northern Portugal (see above). A study of conditions off northwestern Spain has suggested that fish concentration is related to temperature, although both the physical and the biological data are inadequate.

The temperature-controlled distribution of *Brama* may be as follows: The adult fish seem to prefer water with temperatures higher than 55°F (12.8°C), seek water of such temperature at depths from the surface to about 500 meters, and cannot live indefinitely in waters below 50°F (10°C). (The depths of capture reported for the southern catches are in general much deeper than those to the north: the "tropical submergence" of authors and an expected phenomenon.) A part of the oceanic *Brama* population will expand into the North Atlantic as seasonal warming of the upper layers permits. But during the coldest months (in terms of sea-surface temperature) the range will be restricted, if not sharply limited, by a "thermal curtain" separating water colder than *ca.* 55°F (12.8°C) to the north from the warmer waters to the south.

The greatest catch of *Brama brama* is
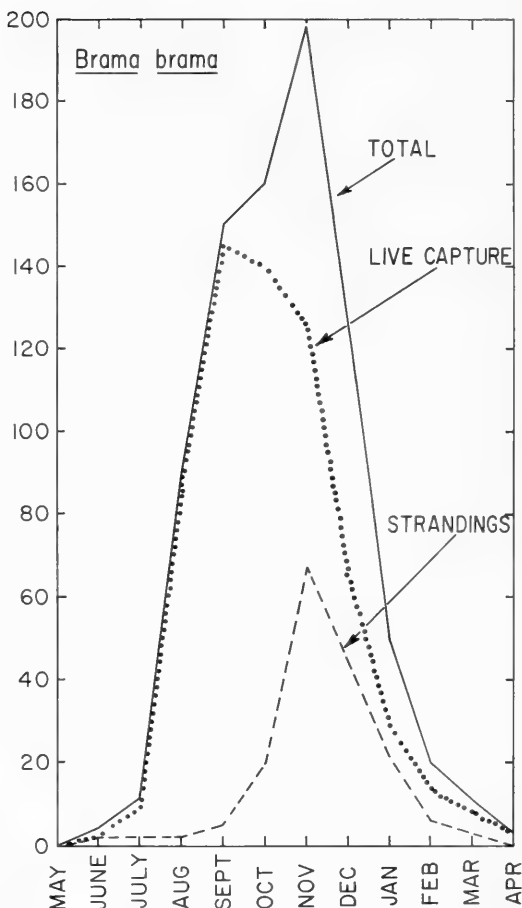
Figure 4. Number of records, from Great Britain northward, of *Brama brama*, by month.

that taken in the area between 41° and 43°N at about 9°W. The most productive month is March (Figure 2), with large but lesser catches during adjacent months. The temperature at a depth of 200 meters is thought not to fluctuate seasonally to any significant extent, and the 200 meter 53.6°F isotherm (12°C, the isotherm nearest our 55°F, or 12.8°C, supposed barrier value) reaches the coast near Vigo (see Figure 5). North of this line *Brama* would be restricted to water less than 200 meters deep throughout the year. Not far north of this, during March, the surface waters become colder
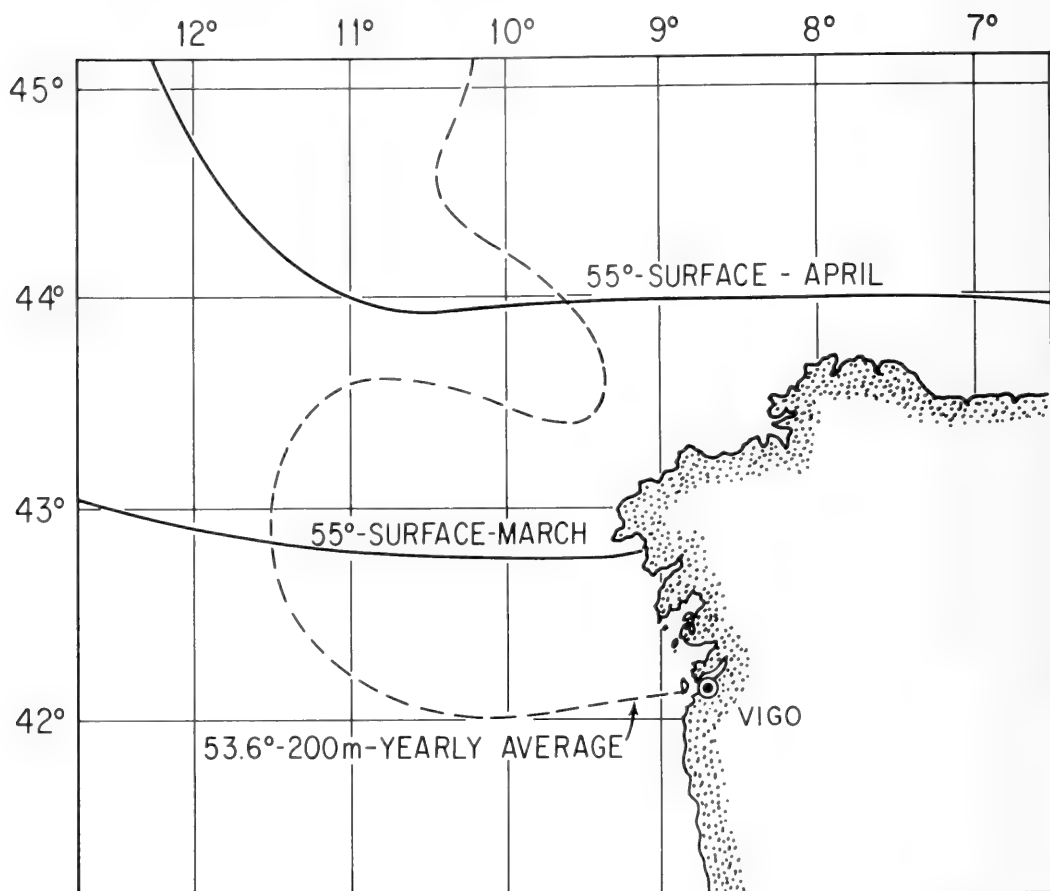
Figure 5. Surface and 200 meter isotherms off northwestern Spain during March and April. Data from Fuglister (1954) and Anonymous (1948).

than 55°F. (The 55°F surface isotherms for March and April are also shown in Figure 5.) Thus, off the corner of Spain there is an east-west temperature barrier, the top of which fluctuates during the winter months (January through March), but does not allow these fish to round Cape Finesterre until April. The bottom of the screen remains stationary, off Vigo, restricting *Brama* to a shallow stratum and preventing the northward escape of the population until the top of the barrier moves northward in April.

An unexpected and unexplained phenom- enon converts this screen into a most effi- cient trap, which could prevent a temper- ature-sensitive population heading north- ward along the coast from changing to any direction save to that from which it came. This can be seen in the three one-degree squares labeled A, B, and C in Figure 6. The month of interest is again March, that of lowest water temperature and greatest *Brama* landings. Square A and that below it contain the fishery. The depth-temperature profile in square A shows that the water column above about 150 meters is nearly uniform in temperature and above 55°F. In
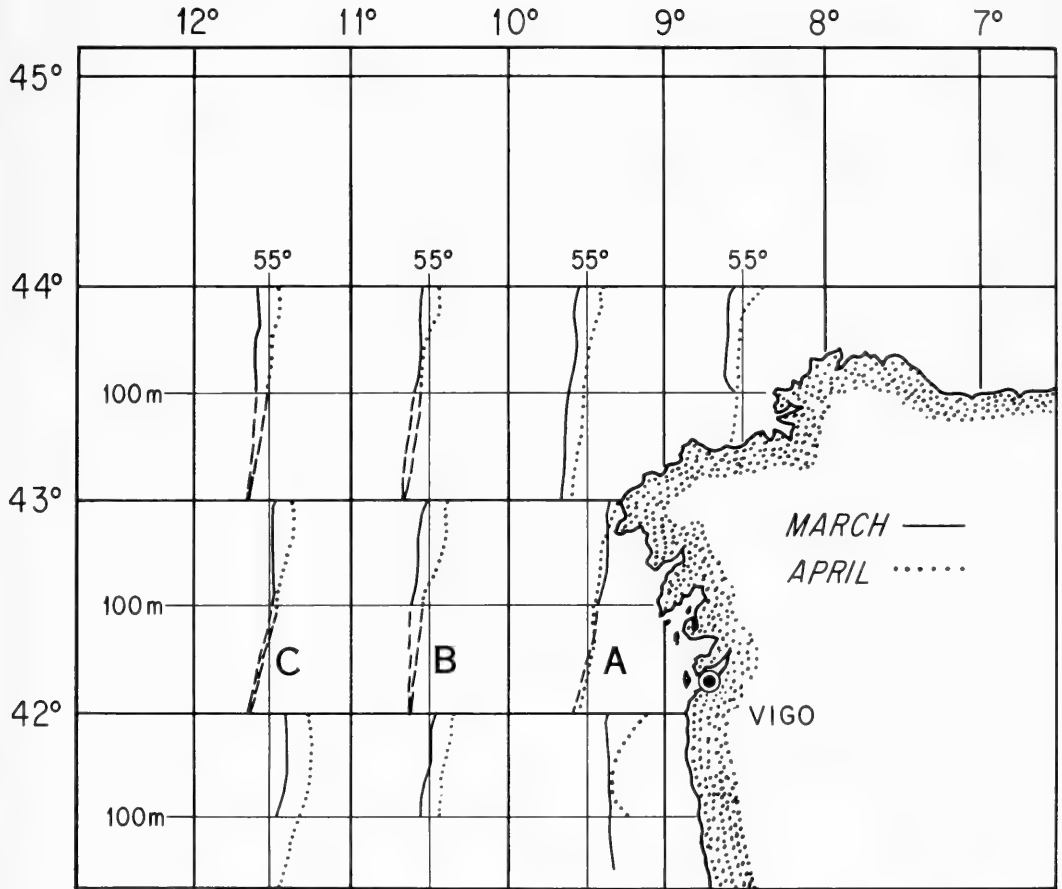
Figure 6. Depth-temperature profiles, March and April, for one-degree squares off northeastern Spain. Broken lines are extrapolations from 100–200 meters, based on 200 meter temperatures (Fuglister, 1954).

square B, the next offshore, this water column is below 55°F in March for all or most of its height—waters which we think are unsuitable for *Brama*. In square C, the next seaward, the water is again amenable to our fishes. Thus that part of the *Brama* population migrating northward along the coast, if limited in distribution by temperature, will be limited to the north *and west* and will be restricted bathymetrically as well. Such a population can do nothing save retreat southward or congregate, to await the later warming of the surface waters and immediate predation by the fishing fleet.

While it is tempting to continue this line of study to account for the abundance of *Brama* off the north coast of Spain in December and January, we will desist; the data are even poorer than those available for the northwest area and the discussion even of this area is based on elusive and incomplete data, generalized temperature curves, poor knowledge of the times and greatest abundance of fish, effect on apparent abundance of variations in fishing effort, complete ignorance of localized hydrographic peculiarities, etc. Nonetheless, the existence of a water column most of which is above 55°F (12.8°C) and the
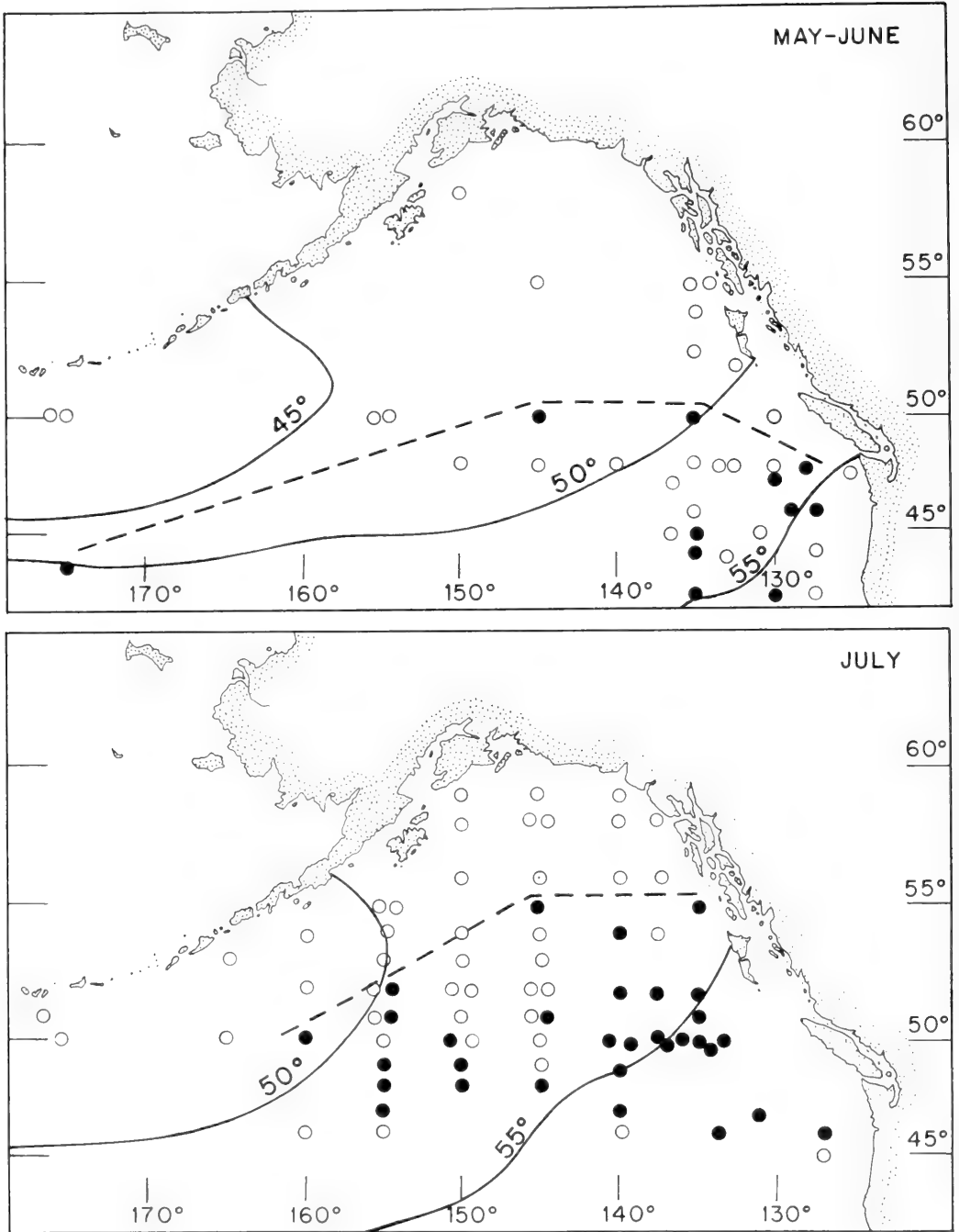
Figure 7. Seasonal northward progression of adult *Brama japonica* and surface isotherms in the northeastern Pacific. ◯ Negative gill-net stations. ● Positive gill-net stations. Data from the exploratory fishing activities of the Canadian and United States Governments. Modified from Neave and Hanavan (1960: 227), with surface isotherms added from the Scripps Atlas (Anonymous, 1948).
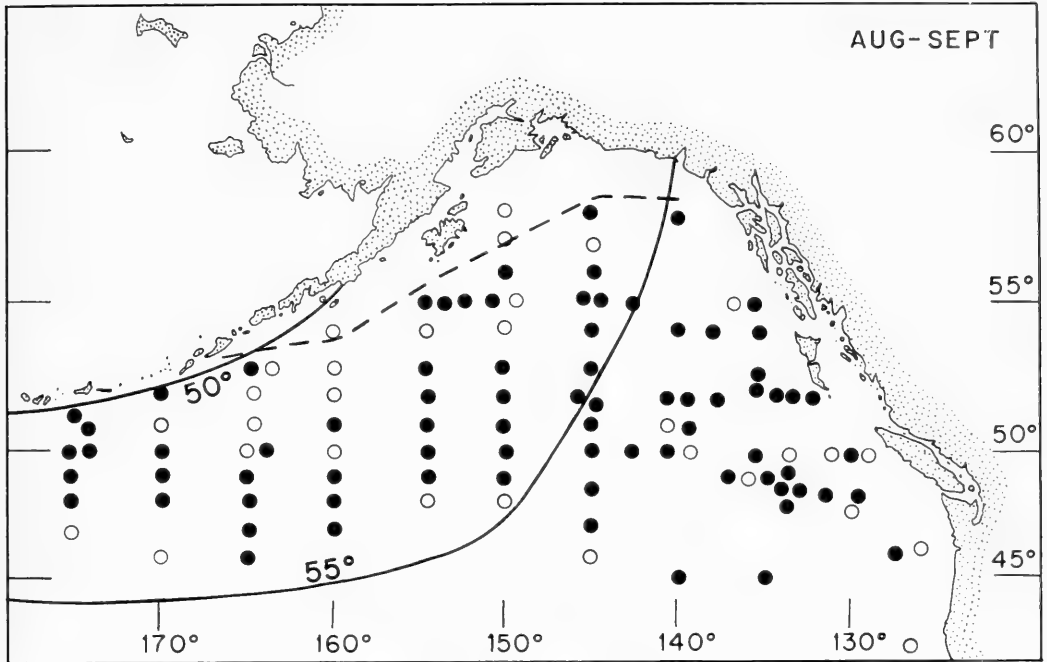
Figure 7 continued

restricting influence of the seasonally-fluc-
tuating 55°F surface isotherm are compati-
ble with the concentration of these fish
along the Spanish coast in the area off Vigo.

DISTRIBUTION OF ADULT BRAMA JAPONICA

The distribution of the North Pacific
Brama japonica between California and the
Aleutian Islands has been reviewed by Hitz
and French (in press, *B. brama* of their
terminology). Young specimens have been
caught off northern Mexico (unpublished
records) and a single catch was made by a
commercial trawler in the Bering Sea (this
specimen is now in the U.S. National Mu-
seum). Young specimens caught during
the cruises of the California Cooperative
Oceanic Fisheries Investigations suggest a
spawning area extending along the coast at
least from 25° to 33°N, although this and
other material from the North Pacific is still
under study. In contrast to the northern

distributional data for the Atlantic *Brama
brama*, which required a literature review
ad nauseam (Table 2), data on the seasonal
distribution and abundance of *B. japonica*
come as a convenient by-product of the
high seas gill-net salmon surveys of recent
years (Powell, Alverson, and Livingstone,
1952; Powell and Peterson, 1957; Hanavan
and Tanonaka, 1959). These are the data
on which the discussions of Neave and Han-
avan (1960) and Hitz and French (in
press) are chiefly based.

There are two ways in which the relation-
ship between this fish and temperature has
been studied. One is that used in the analy-
sis of our Atlantic *Brama brama* data—the
comparison of monthly fish distribution
and surface temperature structure. This is
the approach used by Neave and Hanavan
(1960), who report the minimum and maxi-
mum temperatures, 9.5°C (49.1°F) and
17°C (62.6°F), at which *B. japonica* has
been taken in the Gulf of Alaska, and (p.
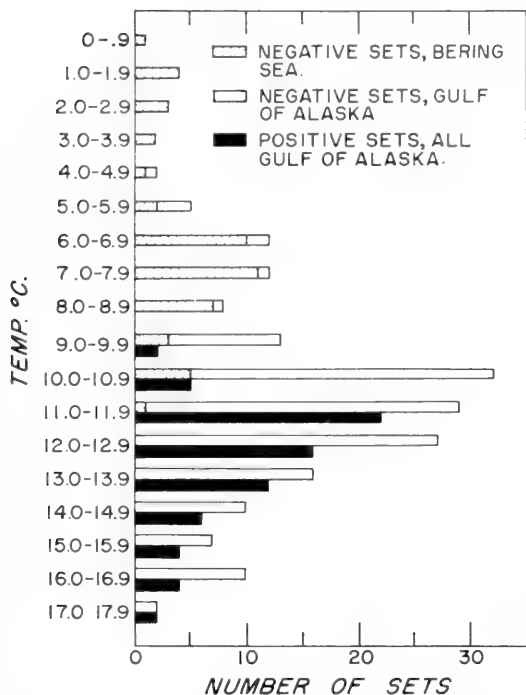
Figure 8.   Temperature and the capture of *Brama japonica* in gill-net sets in the Gulf of Alaska. Data from Hanavan and Tanonaka (1959).

229) plot the captures by period (May–June, July, and August–September). Their charts, to which we have added surface isotherms and otherwise modified, are reproduced here (Figure 7). A seasonal northward progression, correlated with the identical isotherms seen to control the spread of *B. brama* in the North Atlantic, is indicated. The 50°F (10°C) August–September isotherm coincides with the 50°F isothere and with the Aleutian arc. There is but a single recorded instance of an Atlantic *Brama brama* from north of this isothere, and there is but a single record of *B. japonica* from north of this line in the Pacific.

Temperature preference can also be inferred from apparent abundance as reflected in catch data. Number of stations, negative and positive, for *Brama japonica* were plotted against temperature, converted to degrees Centigrade, in Figure 8, using catch data reported by Hanavan and Tanonaka

(1959). These data show highest catches to be in waters warmer than 11°C (51.8°F). Catch-per-shackle of gill-net gear similarly shows that good catches are most frequent between 11°C (51.8°F) and 15°C (59.0°F). Hitz and French (in press), however, note that this unit of effort is undesirable as mesh size, and thus fishing effectiveness, varied among the many sets. These authors thus prudently selected the "set" as the unit of fishing effort and found an apparent peak in relative abundance or availability in gill-net sets (their table 2) in waters of 12–13°C (53.6–55.4°F).

DISCUSSION

There are several indications of parallel, temperature-controlled phenomena in the two closely related species: the migrations into higher latitudes which begin in spring and follow the advance northward of the 50°–55°F (10°–12.8°C) isotherms; the virtual exclusion of all adults from waters north of the 10°C (50°F) isothere; and the more southern spawning ground. But without known Pacific counterpart is the winter congregation of adults off Spain, and we raise here the suggestion that such a congregation may occur. During the winter months, in waters bounded to the east by California and to the north by 10°–12°C surface isotherms, large numbers of *Brama japonica*, which have spawned further south, may be congregating in anticipation of the seasonal warming. Local upwelling may disrupt the situation, but an attempt to locate such congregations if they do occur is in order.

An analysis of the abundant hydrographic data to determine the contour of the 55°F (12.8°C) surface isotherm during the coldest months and the locality where the water column above but not below 150 meters exceeds 55°F would suggest an area in which these fish congregate. This area will be somewhere off central California, and experimental fishing there with a longline fashioned after that used in Spain might be rewarding.

ACKNOWLEDGMENTS

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TABLE 1. SPANISH LANDINGS OF *Brama brama* FROM 1950 THROUGH 1959. Weight, and per cent of total Spanish *Brama* catch, by region; and total catch, with per cent of all fish landed contributed by *B. brama*, for all of Spain. Regions, which correspond to data-reporting units, as follows: Cantábrica: northern Atlantic coast, Bidasoa to Atalaya, including San Sebastian, Bilboa, Santander, etc.; Noroeste: northwestern Atlantic Atalaya to Porcia al Miño incl. La Coruña, Vigo, etc.; Suratlantic: southwestern Atlantic coast, Guadiara to Rio Guadiaro incl. Huelva, Sevilla, Cadiz, etc.; Surmediterránean: Rio Guadiaro to Cape Gata, incl. Estepona, Malaga, Almeria, etc.; Levante: Cape Gata to Cape Nao, incl. Cartegena, Alicante, etc.; Tremontana: Cape Nao to the French border, incl. Valencia, Castellon, Tarrogona, etc.; Balear: Balearic Ids.; Canaria: Canary Ids. Data from published Spanish fishery data (Anon., 1946 *et seq.*)

YEAR		1950	1951	1952	1953	1954	1955	1956	1957	1958	1959
Cantábrica	Metric tons	927.8	1705.9	1662.1	4566.3	3362.1	5848.7	3905.2	2886.5	273.0	71.8
	% Spanish *Brama* catch	16.53	32.38	21.44	36.62	28.61	44.69	30.58	25.07	4.43	0.91
Noroeste	Metric tons	4614.3	3507.4	5933.2	7522.2	8011.9	6796.7	8483.1	8145.6	5388.9	7343.2
	% total *Brama* catch	82.21	66.58	76.54	60.33	68.18	51.94	66.43	70.74	87.4	93.33
Suratlantic	Metric tons	30.8	9.6	39.6	304.2	332.6	383.9	350.6	450.1	428.2	411.9
	% total *Brama* catch	0.55	0.18	0.51	2.44	2.83	2.94	2.75	3.91	6.95	5.24
Surmediterránean	Metric tons	5.5	1.8	–	29.0	25.3	34.2	24.3	26.9	18.2	1.5
	% total *Brama* catch	0.10	0.03	–	0.23	0.21	0.26	0.19	0.23	0.30	0.02
Levante	Metric tons	5.4	3.3	3.3	8.9	5.6	8.2	0.9	2.7	34.5	3.6
	% total *Brama* catch	0.10	0.06	0.04	0.07	0.05	0.06	–	0.02	0.56	0.05
Tremontana	Metric tons	3.2	1.5	2.7	0.8	0.7	0.6	–	0.2	–	–
	% total *Brama* catch	0.05	0.03	0.04	0.01	0.01	–	–	0.2	–	–
Balear	Metric tons	3.7	0.1	0.1	–	–	–	–	–	0.2	–
	% total *Brama* catch	0.06	–	–	–	–	–	–	–	–	–
Canaria	Metric tons	22.4	39.0	110.6	36.8	13.2	14.7	6.5	3.0	22.3	35.6
	% total *Brama* catch	0.40	0.74	1.43	0.30	0.11	0.11	0.05	0.03	0.36	0.45
Spanish totals	Metric tons (rounded off)	5613	5269	7752	12468	11751	13087	12771	11515	6165	7868
	% all fish landings	1.24	1.11	1.72	2.66	2.50	2.34	2.30	1.98	1.01	1.23

TABLE 2. THE KNOWN RECORDS OF CAPTURE, THROUGH 1961, OF ADULT *Brama brama* IN THE WESTERN ATLANTIC AND IN THE EASTERN NORTH ATLANTIC NORTH OF THE BAY OF BISCAY. (T.L. = TOTAL LENGTH; F.L. = FORK LENGTH; S.L. = STANDARD LENGTH)

JANUARY

DATE	NO. (AND SEX)	LENGTH (CMS)	LOCALITY	CIRCUMSTANCES	AUTHORITY AND REMARKS
I 39	1	39	Vestmannaeyjar, Iceland		Saemundsson, 1949: 18
15 I 14	1	43 t.l.	Grindavik, S.W. coast Iceland	Stranded alive	Saemundsson, 1922: 180
23 I 1850	1	39.5 s.l.	Faroes		Nielsen, 1961, pers. comm.
I 50	1	46	Mouth of Zolotoi River, 100 km. E. of Kolskii Inlet, Murmansk, U.S.S.R.	Stranded dead	Andriashev, 1954: 215, citing I. I. Laru-nov in "Polyarnaya Pravda."
8 I 50	1	52 t.l.	Austevik, Avaldsnes, Karmöy, Norway	On the shore	Holgersen, 1950: 89
5 I 50	1	58.5 t.l.	Skjoldastraumen, Skjold, N. Ryfylke, Rogaland, Norway	Fishing line (jig)	"
19 I 52	1	53 (t.l.?)	Klepp, Reve, Rogaland, Norway	On shore	"
7 I 57	1 ♂	54.5	3–4' off Whitehills, Moray Firth	Seine	Rae and Lamont, 1959: 85; + details pers. comm.
16 I 57	1	53.0	Off Tolsta Head, Lewis	Drift net	"
31 I 56	1	53.5	Loch Ainort, Isle of Skye	Stranded	Rae and Wilson, 1958b: 96; + details pers. comm.
5 I 56	1 ♀	59.0	Pennan, Moray Firth	Scooped from the sea	"
7 I 53	5		Finkenwärder-allee (ca. 60°N., 3°E.)	Comm. landing	Kotthaus, 1954: 117
30 I 50	1 ♀	58.2	near Lath, Moray Firth	Stranded	Rae and Wilson, 1951: 83; + details pers. comm.
I 50	2		59°N. (200 m.)	Caught	Kristensen, 1950: 50
10 I 09	1	56	North Berwick beach, E. Lothian	Stranded	Ingles, 1909: 118
14 I 52	1		Snaresund, Aust-Agder, Norway		Willgohs, 1954: 4
I 53	1	51.5 t.l.	Langesundfjord, Telemark, Norway	Fishing line	"
28 I 53	1	59 t.l.	Fjeldskaar, Lindesnes, Vest-Agder, Norway	Found dead in shallow water	Willgohs, 1954: 4
I 56	1	47	58°40'N., 3°20'E.	Caught	Verwey, 1958: 542–3
18 I 28	1	56	Hirsholmene, Denmark	Stranded	Jensen, 1940: 195–7
10 I 38	1 ♀	58.5	near Helmsdale, Moray Firth	Stranded	Rae and Lamont, 1962, pers. comm.
6 I 09	1		15' S.E. Aberdeen	Caught	Thompson, 1918: 63–64; + details; Rae and Lamont, 1962, pers. comm.
15 I 10	1		4–5' E.N.E. Aberdeen	"	"
11 I 11	1		9' E.N.E. Aberdeen	"	"
12 I 11	1		14' S.S.E. Aberdeen	"	"

Date	No.	Size	Location	Condition	Reference
12 I 11	1		7–8' S.S.E. Tod Head, Kincardine	"	Rae and Lamont, 1962, pers. comm.
12 I 11	1		14' S.E. Tod Head, Kincardine	"	Thompson, 1918: 63–64; + details; Rae and Lamont, 1962, pers. comm.
16 I 11	1		16' S. × E. Aberdeen	"	
19 I 11	1		12' S.S.E. Aberdeen	"	"
20 I 11	1		25' N. × E. Rattray Head, Aberdeen	"	"
20 I 11	1		6' E. × S. ½ S. Aberdeen	"	"
14 I 11	1		7' E. × N. Aberdeen	"	"
I 52	1	51–60	Dutch coast around Haarlem, Holland	Stranded	Verwey, 1953: 346–7
I 56	1	55	between Katwijk and Texel, Holland	Stranded	Verwey, 1958: 542–3
I 57	1	53	Scheveningen, Holland	Stranded	Verwey, 1960a: 548–9
I 58	1♂	53	Texel Hole, W. of Texel, Holland	Caught	Verwey, 1960b: 564–5
3 I 50	1	60	near Egmond, Holland	Stranded alive	Kristensen, 1950: 50
9 I 50	1	45	Texel, Holland	Stranded	"
10 I 50	1		Texel, Holland	Stranded alive	"
12 I 50	1	42	Texel, Holland	Stranded alive	"
12 I 50	1	48	near Scheveningen, Holland	Stranded alive	"
16 I 50	1♂	46.5	Texel, Holland	Stranded	"
18 I 50	1♂	56	near Huisduinen, Holland	Stranded	"
25 I 1847	1		near Great Yarmouth, Norfolk	Stranded (?)	Patterson, 1897: 548
17 I 28	1		near Flamborough Head, Yorks.	Brought up in the trawl; dead and decomposed	Clarke, 1928: 108

FEBRUARY

Date	No.	Size	Location	Condition	Reference
26 II 51	1	46.5 t.l.	Tustna, Nord-Møre, Norway	Fishing line	Willgohs, 1954: 4, citing Nordgård, 1928: 63–4
9 II 52	1	51 t.l.	Viste, Randaberg, Rogaland, Norway	On shore	Holgersen, 1959: 128; Willgohs, 1954: 4, citing Holgersen, 1950 and pers. comm.
1 II 56	2	54; 55	N. North Sea	Comm. landings	Kotthaus, 1958: 96
1 II 57	1		Heiastrandbukta, near Farsund, Norway	Mackerel net (3 fm)	Holgersen, 1959: 128
2 II 53	1	55	edge of Norwegian Deep, ca. 60°N.	Comm. landings	Kotthaus, 1954: 117
1 II 56	1♂	52.3	Peterhead, Aberdeen	Stranded	Rae and Wilson, 1958b: 96; + details pers. comm.
12 II 56	1♂	51.0	Whitehills, Moray Firth	Stranded	"
28 II 50	1♂	53.0	Gardenstown, Moray Firth	Salmon net	Rae and Wilson, 1951: 83; + details pers. comm.
14 II 53	1♀	55.5	11' N.W. × W. Muckle Flugga, Shetland	Trawl	Rae and Wilson, 1954b: 117; 1954a: 178

TABLE 2. *Continued*

DATE	NO. (AND SEX)	LENGTH (CMS)	LOCALITY	CIRCUMSTANCES	AUTHORITY AND REMARKS
8 II 50	1		Røvaer, Rogaland, Norway		Holgersen, 1950; + pers. comm. citing Willgohs, 1954: 4
II 56	1 ♂	50	58°40'N., 3°20'E.	Caught	Verwey, 1958: 542–3
22 II 53	1	54	Viking Bank	Trawl	Krefft, 1961, pers. comm.
II 50	1	43.5	59°20'N., 3°30'E.	Caught	Kristensen, 1950: 50
15 II 09	1		45' E. × N. Wick, Caithness	Caught	Thompson, 1918: 63–4; Rae and Lamont, 1962, pers. comm.
22 II 09	1		11' N.E. Foula, Shetland	Caught	"
20 II 15	1		40' S.E. Aberdeen	Caught	"
II 56	1 ♀	51	between Katwijk and Texel, Holland	Stranded	Verwey, 1958: 542–3
12 II 50	1 ♀	40	near Wassenaar, Holland	Stranded (?)	Kristensen, 1950: 50
II 56	1		Mouth of R. Moy, Co. Mayo, Ireland	Washed ashore	Roche, 1956: 109

MARCH

DATE	NO. (AND SEX)	LENGTH (CMS)	LOCALITY	CIRCUMSTANCES	AUTHORITY AND REMARKS
13 III 56	1	54 (t.l.?)	Vågsfjorden, Norway		Holgersen, 1959: 128
28 III 56	1	50 (t.l.?)	W. of Vealbygd, Karmøy, Norway		"
1 III 51	1		Larviksfjorden, Norway		"
1 III 50	1 ♂	45.0	near Cullen, Moray Firth	Salmon net	Rae and Wilson, 1951: 83; + details pers. comm.
4 III 50	1		near Langesund, Telemark, Norway	On the shore	Willgohs, 1954: 4
2 III 50	1	57 t.l.	Stråholmen, Langesund-Drev, Norway		Oslo Museum
2 III 09	1		between Flannans and Butt of Lewis	Caught	Thompson, 1918: 63–4; + details, Rae and Lamont, 1962, pers. comm.
1 III 11	1		10–12' S.E. Aberdeen	Caught	"
III 50	1		55°N., 6°02'E.	Comm. trawler (43–45 m)	Krefft, 1961, pers. comm.
III 1891	1	50.8	Portscatho, Cornwall	Taken with a gaff	Clark, 1907: 426
12 III 05	1		near St. Anthony Lighthouse, Falmouth, Cornwall	Thrown up dead after violent storm	"

APRIL

DATE	NO. (AND SEX)	LENGTH (CMS)	LOCALITY	CIRCUMSTANCES	AUTHORITY AND REMARKS
IV 51	1	49 t.l.	Hennøystrand, Sogn og Fjordane, Norway	Caught by fishing net (70 m)	Willgohs, 1954: 4

9 IV 52	1		Muckle Flugga, Shetland	Comm. trawler (250 m)	Krefft, 1961, pers. comm.
8 IV 25	1	47	280′ N.E. Buchanness	Trawl	Rae and Lamont, 1962, pers. comm.
			JUNE		
VI 22	1	66 t.l.	Grindavik, S.W. coast of Iceland	Cast ashore dead	Saemundsson, 1927: 162
18 VI 51	1	39.5 t.l.	Tampen, *ca.* 143 kv/mil west of Rundøy, Norway	Caught	Zoological Museum, Univ. of Bergen
3 VI 1893	1		Dungarvon, Co. Waterford, Ireland	Caught	Crane, 1893: 230
12 VI 1875	1	"full-size"	Western Beach, Penzance, Cornwall	Floundering in shallow water; alive but exhausted	Cornish, 1875: 4542
			JULY		
15 VII 19	1	58	Vestmannø Rhed, Iceland	Taken alive	Saemundsson, 1922: 180
28 VII 59	1♀	59	7–8′ W. of Suderø, Faroes	Trawl	Rae and Lamont, 1961: 105; + details, 1962, pers. comm.
16 VII 24	1		20′ E.S.E. of Rockall	Longline	Rae and Lamont, 1962, pers. comm.
23 VII 24	1		115′ S.W. of Rockall	Longline	"
23 VII 25	1		100′ S.W. of Rockall	Longline	"
16 VII 26	1♀	59	100′ S.W. of Rockall	Caught	"
28 VII 27	1		56′ S.S.W. of Rockall	Caught	
18 VII 57	2 (1♂ = 55.5)		George Bligh Bank	Longline	Rae and Lamont, 1959: 85; + details, 1962, pers. comm.
4 VII 1866	1		Looe, Cornwall	Washed ashore alive	Clogg, 1866: 349
10 VII 1874	1		near Penzance, Cornwall	Stranded nearly dead	Cornish, 1874: 4266
VII 1878	1	38	Portrush, Ireland	Found dead	Ogilby, 1885: 514–15
			AUGUST		
15 VIII 52	1		S.W. Syderø, Faroes	Trawl	Rae and Wilson, 1953b: 39; 1953a: 147
VIII 52	2♂	60.4	Faroe Bank	Longline	"
28 VIII 52	1		Skeidaraardeep, Iceland	Comm. landings	Brandes, Kotthaus and Krefft, 1953: 47
25 VIII 53	1		Rose Garden, Iceland–Faroes Ridge	Comm. landings	Brandes, Kotthaus and Krefft, 1954: 44
VIII 51	1	54.5	25′ S. of Munken Rock, Faroes	Longline	Rae and Wilson, 1952b: 56; 1952a: 107
15 VIII 19	1	58 t.l.	Vestmannø Rhed, Iceland	Caught living (trawl?)	Saemundsson, 1922: 180

TABLE 2. *Continued*

Date	No. (and Sex)	Length (cms)	Locality	Circumstances	Authority and Remarks
21 VIII 53	28		Vestmannaeyja, Iceland, 21°W.	Comm. landings	Brandes, Kotthaus and Krefft, 1954: 44
27 VIII 51	1		Ingolfshöfdi, Iceland	Comm. landings	Brandes, Kotthaus and Krefft, 1953: 47
28 VIII 51	1		Ingolfshöfdi, Iceland	Comm. landings	"
10 VIII 54	1	57	Sido Ground	Comm. landings	Brandes, Kotthaus and Krefft, 1956: 30
15 VIII 54	1	54.5	Skafta Deep, Iceland	Comm. landings	"
13 VIII 27	3		35' S. of Sumbo Lt, Faroes		Rae and Lamont, 1962, pers. comm.
30 VIII 27	2		S.E. corner Faroe Bank		"
4 VIII 24	1		70' W.S.W. of Rockall	Caught	"
5 VIII 24	2		8' S.W. of Rockall	Caught	"
14 VIII 24	1		115' S.W. of Rockall	Caught	"
3 VIII 25	1		27' N.N.W. of Rockall	Caught	"
11 VIII 26	3		25' N.N.E. of St. Kilda	Caught	"
23 VIII 26	2		46' N.W. × W. of Barra Head	Caught	"
31 VIII 26	1		25' S.E. × ½ S. of Sula Sgeir (off N.W. Scotland)	Caught	"
3 VIII 27	1		50' S.S.W. Rockall	Caught	"
27 VIII 28	1		Lousy Bank	Caught	"
27 VIII 49	1		40-45' N.E. × N. ½ N. of North Rona	Caught	"
9 VIII 52	1	54	Muckle Flugga, Shetland	Longline	Krefft, 1961, pers. comm.
15 VIII 52	2♂	56.5	Bill Bailey's Bank	Trawl (250 m)	Rae and Wilson, 1953b: 39; 1953a: 147
8 VIII 50	2♂ / 2♀	49.2; 53.5 / 51.5; 53.5	10-12' W.N.W. of St. Kilda	Longline / Comm. long-liner	Rae and Wilson, 1951: 83; Rae and Lamont, 1962, pers. comm.
21 VIII 57	2		Lousy Bank	Longline	Rae and Lamont, 1959: 85: + details, 1962, pers. comm.
3 VIII 57	1		Lousy Bank	Longline	Rae and Lamont, 1960: 78: + details, 1962, pers. comm.
7 VIII 58	1	59.7	Rockall	Longline	"
8 VIII 55	4		Rockall Bank	Longline	Rae and Wilson, 1957: 103; 1956a: 100
27 VIII 59	1♂	54	Noup Deep, W. Orkney	Trawl	Rae and Lamont, 1961: 105; + details, 1962, pers. comm.
29 VIII 59	2		Muckle Flugga, Shetland	Trawl	
VIII 1821	1	43	Looe, Cornwall	Live caught at surface	Couch, 1822: 78; 1849: xxvii-xxviii
VII-VIII 1886	1		Newlyn Harbour, Penzance, Cornwall	Captured by boathook through the eye, while swimming in pool	Cornish, 1886: 371

Date	No.	Sex	Length	Locality	Capture	Reference
VIII 50	1		36	Polperro, Cornwall	Longline	Brandes, 1952: 39
3 VIII 60	1		58	George Bligh Bank	Trawl	Rae and Lamont, 1962, pers. comm.
24 VIII 61	1	♀	484 f.l.; 572 t.l.	North Sound of Galway Bay, Ireland	Trawl	Gilson, 1962: 15–17
24 VIII 61	1	♀	459 f.l.; 565 t.l.	North Sound of Galway Bay, Ireland	Trawl	"
24 VIII 61	1	♀	477 f.l.; 576 t.l.	North Sound of Galway Bay, Ireland	Trawl	"
24 VIII 61	1	♀	500 f.l.; 612 t.l.	North Sound of Galway Bay, Ireland	Trawl	"
24 VIII 61	1	♂	500 f.l.; 600 t.l.	North Sound of Galway Bay, Ireland	Trawl	"
24 VIII 61	1	♂	485 f.l.; 592 t.l.	North Sound of Galway Bay, Ireland	Trawl	"
24 VIII 61	1	♂	422 f.l.; 517 t.l.	North Sound of Galway Bay, Ireland	Trawl	"
24 VIII 61	1		466 f.l.; 555 t.l.	North Sound of Galway Bay, Ireland	Trawl	"
24 VIII 61	1		477 f.l.; 576 t.l.	North Sound of Galway Bay, Ireland	Trawl	"

SEPTEMBER

Date	No.	Sex	Length	Locality	Capture	Reference
2 IX 53	1			Rose Garden, Iceland–Faroes Ridge	Comm. landings	Brandes, Kotthaus and Krefft, 1954: 44
8 IX 53	50–60			Vestmannaeyja, Iceland	Comm. landings	"
14 IX 53	3			Rose Garden, Iceland–Faroes Ridge	Comm. landings	"
28 IX 53	3			S.W. Iceland	Comm. landings	"
30 IX 53	6			Vestmannaeyja, Iceland	Comm. landings	"
1 IX 57	3		52–58	S.W. Iceland	Comm. trawler	Brandes and Kotthaus, 1959: 42
10 IX 57	2		55; 58	63°14'N., 24°50'W.	Comm. trawler	"
14 IX 57	2		56; 58	Gamelloch, N.W. Iceland	Comm. trawler	"
5 IX 52	1			Ingolfshófdi, Iceland	Comm. landings	Brandes, Kotthaus and Krefft, 1953: 47
14 IX 52	1			Rose Garden, Iceland–Faroes Ridge	Comm. landings	"
15 IX 52	4			Ingolfshófdi, Iceland	Comm. landings	"
16 IX 52	1			Ingolfshófdi, Iceland	Comm. landings	"
18 IX 52	1			Berudeep, Iceland	Comm. landings	"

TABLE 2. Continued

Date	No. (and sex)	Length (cms)	Locality	Circumstances	Authority and Remarks
5 IX 54	1♀	62	63°07'N., 23°53'W.	Comm. landings	Brandes, Kotthaus and Krefft, 1956: 30
25 IX 56	1		Syderø Bank, Faroes	Longline	Rae and Wilson, 1958a: 54
13 IX 58	1	56	Rose Gardens, Iceland–Faroes Ridge	Comm. trawler	Brandes and Kotthaus, 1960: 72
6 IX 01	1	46.5 t.l.	Selvogur, S. coast of Iceland	Ashore after S.E. storm	Saemundsson, 1903: 46
6 IX 51	1		63°15'N., 20°05'W.	Comm. landing	Brandes, Kotthaus and Krefft, 1953: 47
8 IX 08	1	49 t.l.	Grindavik, S.W. coast Iceland	Stranded alive	Saemundsson, 1922: 180
IX 30	1	33.5 t.l.	Grindavik, S.W. coast Iceland	Stranded	Saemundsson, 1939: 191
2 IX 57	1 ♂	57.0	Faroe Bank	Longline	Rae and Lamont, 1959: 85: + details pers. comm.
19 IX 56	2♀	53.6	45' N.N.W. of Butt of Lewis	Longline	Rae and Wilson, 1958b: 96: + details pers. comm.
IX 51	8 cwts		50' W. × N. Barra Head	Longlines	Rae and Wilson, 1952a: 107
30 IX 50	1		28' S.E. × E. of Aberdeen	Comm. trawler	Rae and Wilson, 1951: 83: + details, 1962, pers. comm.
IX 38	1		W. of Shetland	Caught by dogfish line	Willgohs, 1954: 4
24 IX 31	1		Kattegat, N. of Laesø	Caught	Jensen, 1940: citing Jägerskiöld, 1932: 39
10 IX 59	1♂	61	21' N.W. × W. of Muckle Flugga, Shetland	Trawl	Rae and Lamont, 1961: 105: + details, 1962, pers. comm.
23 IX 59	2♀	60; 61	40' N.W. of Sule Skerry	Trawl	"
12 IX 59	1		off Ronas Voe	Trawl	
12 IX 54	1		10' N. Muckle Flugga, Shetland	Trawl	Rae and Wilson, 1956b: 69
28 IX 54	1		Butt of Lewis	Longline	"
13 IX 59	{1♀ 59 / 1♂ 57}		18–20' W.N.W. of Flugga, Shetland	Trawl	Rae and Lamont, 1961: 105: + details, 1962, pers. comm.
11 IX 24	1		80' S.W. × W. Barra Head		Rae and Lamont, 1962, pers. comm.
18 IX 25	1		Inverness Firth		"
22 IX 23	3	54; 53; 49	65' W. ¾ S. of Barra Head	Longline	"
30 IX 25	1♂	58	47' N.W. × N. ½ N. of Butt of Lewis	Longline	"
7 IX 26	1		50–60' W.S.W. of Barra Head	Longline	"
29 IX 26	1		45' N.W. ½ W. Barra Head		"
17 IX 28	1		25' N.N.W. of Rona		"
9 IX 36	2♂	60.3; 56.5	50' N.W. × N. Butt of Lewis	Longline	"
22 IX 36	1♂	58	12' N.E. × N. Flugga, Shetland	Trawl	"
8 IX 37	4		30' S.W. × W. of St. Kilda		"
22 IX 37	1		90'–100' N.E. × N. Buchanness		"

12 IX 47	1	61	Basta Voe, Yell, Shetland	Stranded	"
23 IX 49	1		40' N.N.E. of NorthRona	Longline	"
29 IX 49	1		45' N.N.W. Butt of Lewis	Longline	"
25 IX 61	1	60.2	off Flugga	Trawl	"
ca. 29 IX 61	1	62	Shetland area	Longline	
12–13 IX 23	7	55–65	80' W.S.W. of Penmarch Point (N. of St. Nazaire)	Caught on tunny line	Legendre, 1924: 220–221
14 IX 23	6	46; 47; 50; 51; 2 × 52	about 50' W. of Glenan Is. (off Concarneau)	Caught on tunny line	"
IX 51	1		Porcupine Bank (S.W. Ireland)	Commercial	A. C. Wheeler, 1961, pers. comm.
29 IX 52	1		Holbaek Fjord, Zealand, Denmark	(Stranded?)	Zoological Museum, Univ. of Copenhagen
20 IX 57	1	58.7 t.l.; 49.3 f.l.	3' W. of Smerwick Harbour, Ireland	Mackerel nets	Went, 1958: 246
9 IX 33	1		off Scarborough, Yorks.	Taken in trawl net	Clarke, 1934: 24
IX 50	1	37	Porcupine Bank (off S.W. Ireland)	Captured	Brandes, 1952: 39
2 IX 61	1		Dingle Bay, Ireland	Trawl net	Went, 1962: 34
IX 09	1		Courtmassherry, Co. Cork, Ireland		Went, 1962, pers. comm.
15 IX 26	1		19' N.W. × W. of Eagle Island, Ireland		Rae and Lamont, 1962, pers. comm.

OCTOBER

13 X 52	1	55.5	Iceland–Faroes Ridge	Commercial trawler	Krefft, 1961, pers. comm.
2 X 58	3	(1 = 51)	63°16'N, 25°30'W., S.W. Iceland–Mehlsack	Trawler (315 m)	Krefft, 1960: 71; 1961, pers. comm.
13 X 58	2	54; 56	65°10'N, 25°W.	Comm. trawler	Brandes and Kotthaus, 1960: 72
1 X 53	1		Vestmannaeyja, Iceland	Comm. landings	Brandes, Kotthaus and Krefft, 1954: 45
15 X 53	1		10' W. of Vestmannaeyja	Comm. landings	"
X 51	1	54.8 t.l.	about 42' W.N.W. of Storholmen, Norway	Caught (about 290 m)	Willgohs, 1954: 4
ca. 1 X 61	2		Faroe Bank	Longline	Rae and Lamont, 1962, pers. comm.
29 X 52	1	56	10' E.S.E. Aberdeen	Trawl	Rae and Wilson, 1953a: 147; 1953b: 138
31 X 52	1		12–15' N.N.E. Flugga, Shetland	Trawl	"
X 55	1	51–63	58°N, 0°3'E.		Verwey, 1956: 96–97
X 20	1	60	Als, Østjylland, Denmark	Commercial (15 fm)	Jensen, 1940: 194, citing Dansk Fiskeritidende, 1920: 536
21 X 27	1	58 t.l.	Thisted, Denmark	Commercial; live caught in shallow water	Jensen, 1940: 194
8 X 27	1		Frederikshavn, Denmark	Net (10m)	"

TABLE 2.   Continued

Date	No. (and Sex)	Length (cms)	Locality	Circumstances	Authority and Remarks
14 X 27	1		near Fornaes Fyr, Denmark		"
20 X 27	1		Klitmøller, Denmark		"
27 X 27	1		Lokken Strand, Jammer Bugt, Denmark	Stranded after storm	
31 X 27	1		Skagen Sønderstrand, Denmark	Stranded	Jensen, 1940: 195
17 X 29	1		Hansted, Denmark, near land		Jensen, 1940: 195, citing Dansk Fiskeritidende, 1928: 524
22 X 28	1		Torup Strand, Jammer Bugt, Denmark		Jensen, 1940: 196
17 X 36	1		Lild Strand, Denmark		"
13 X 37	1		Aebeltoft, Denmark		
21 X 57	1	55	S.W. coast Norway		Brandes and Kotthaus, 1959: 42
4 X 58	1	58 (t.l.?)	Utsira, Norway		Holgersen, 1959: 128
26 X 53	1		N.N.W. Flugga, Shetland		Rae and Wilson, 1954a: 178
28 X 27	1	59–61	Hunspoint, Queensferry, Firth of Forth	Trawl (65 fm)	Stephen, 1928: 28
28 X 27	1	59–61	Firth of Forth	Caught	"
X 27	1	59–61	Firth of Forth	Caught	"
X 27	1	59–61	180' E.N.E. Girdleness (the Patch)	Caught	
X 51	1		80' N.E. × N. Buchanness	Trawl	Rae and Wilson, 1952a: 107
13 X 52	1		20' E. Flugga, Shetland	Trawl	Rae and Wilson, 1953a: 147; 1953b: 138
16 X 52	1 ♀	54	120' N.E. × N. Buchanness	Trawl	"
16 X 52	2 ♀ ♂	58.5: 61	100' N.E. Buchanness	Trawl	"
17 X 52	1 ♀	58.7	96–110' N.E. ½ N. to E.N.E. Aberdeen	Trawl	"
21 X 52	1 ♀	52.8	15–20' S.E. Fair Isle	Trawl	"
28 X 52	1 ♀	57.5	7' E. Outer Skerries, Shetland	Trawl	
6 X 59	1	58	off Fair I., Scotland	Trawl	Rae and Lamont, 1961: 105; + details pers. comm.
26 X 56	1		Aberdeen Bay	Trawl	Rae and Wilson, 1958b: 96; + details pers. comm.
15 X 53	2		60' N. Sule Skerry (off N.W. Scotland)	Longline	Rae and Wilson, 1954a: 178
X 51	5		40' N.W. Butt of Lewis	Longline	Rae and Wilson, 1952a: 107; 1952b: 116
X 51	1		N.W. × N. Dennis Head, Orkney	Comm. landings (182 m)	"
3 X 53	6		45' N.N.W. Butt of Lewis	Longline	Rae and Wilson, 1954a: 178
19 X 54	1		Muckle Flugga, Shetland	Trawl	Rae and Wilson, 1956b: 69
14 X 57	1		North Minch	Drift net	Rae and Lamont, 1959: 85; 1962, pers. comm.

Date	No.	Measurement	Locality	Method	Reference
15 X 57	1	58.4	off Kebock Head, Lewis	Drift net	Rae and Wilson, 1957: 103; 1956a: 100
14 X 55	1		Cape Wrath, Sutherland	Trawl	Rae and Lamont, 1959: 85; pers. comm.
31 X 57	2	53.3	Joppa, Firth of Forth	Stranded	Rae and Lamont, 1960: 78; pers. comm.
13 X 58	1♀	56.2	5' E.N.E. of Lossiemouth, Moray Firth	Seine net	Rae and Lamont, 1959: 85; pers. comm.
4 X 57	1♀	55.2	Aberdeen Bank	Trawl	Rae and Lamont, 1959: 85; pers. comm.
26 X 56	1		Bell Rock (off St. Andrews)	Trawl	Rae and Wilson, 1958b: 96; pers. comm.
X 27	1	58	Viking Bank (60°20'N., 2°40'E.)	Caught	Grimpe, 1929: 163, citing Ehrenbaum, 1928
18 X 27	2	56; 57	55°10'N, 0°55'E.	Caught (60–70 m)	Harris, 1851: 3301–2
24 X 1851	1♀	57.2	Gardenston Harbour, Cairnie, Banffshire	Swimming inshore at ebb tide—thrown ashore by fisherman with his hands	"
5 X 61	1♀	51.4 t.l.; 44 f.l.; 40.6 s.l.	55°35'N, 1°18'E.	Motorlugger–herring trawl	Krefft, 1961, pers. comm.
5 X 61	1♂	54.7 t.l.; 47.1 f.l.; 42.6 s.l.	55°35'N, 1°18'E.	Motorlugger–herring trawl	"
1 X 25	1		6' S.S.E. of Copinsay, Orkney	Caught	Rae and Lamont, 1962, pers. comm.
9 X 25	1		46' W. ½ S. of Barra Head, Lewis		"
4 X 26	1		18–20' S.E. of Sumburgh Head, Shetland		Rae and Lamont, 1962, pers. comm.
10 X 27	1		26' S.E. × E. of Sumburgh Head, Shetland		"
11 X 27	1		8' S.S.E. of Sumburgh Head, Shetland		"
2 X 28	1		85' S.W. × W. ½ W. of Barra Head, Lewis		"
9 X 28	1		Lousy Bank (S. end)		"
29 X 29	1		14' S.W. of Fair Isle		"
13 X 29	2	65; 64	6' S.E. of Buchanness		"
3 X 31	1		50' E. of Outer Skerries, Shetland		"
18 X 31	1♂	62.5	Aberdeen Beach	Stranded	"
13 X 32	1		20' W. ½ S. of St. Kilda	Longline	"
5 X 33	1		60–75' E.S.E. of Aberdeen	Longline	"
29 X 34	1		7' S.S.E. Sumburgh Head, Shetland		"
3 X 36	1		30' N.N.E. of Buchanness		"
5 X 36	1		110' S.W. × W. of Rockall		"
1 X 49	1♂	44	45' N.N.W. of Butt of Lewis	Longline	"
16 X 49	1♀	60.5	Dounroch Firth, Sutherland	Stranded	"
20 X 49	12		45' N.W. × N. Butt of Lewis	Longline	"

TABLE 2. Continued

Date	No. (and Length cms)	Locality	Circumstances	Authority and Remarks
22 X 49	2	90–95' E.N.E.–N.E. × E. Aberdeen	Trawl	"
24 X 49	1♂ 59	18' N.N.W. Fair Isle	Trawl	"
18 X 60	1♀ 60	45' N.W. of Butt of Lewis	Longline	"
19 X 60	1♀ 63.5	3' S. of Golspie, Moray Firth	Probably stranded	"
29 X 60	1♀ 60.2	Stonehaven Beach, Aberdeen	Stranded	"
ca. 1 X 61	1♀ 58.2	off Flugga, Shetland	Trawl	"
3 X 61	1	off Sumburgh Head, Shetland	Stranded	"
9 X 61	2	The Reef (58°30'N., 3°E.)	Trawl	"
17 X 61	1♀ 62.5	50' N.W. of Sule Skerry	Longline	"
X 51 4 cwts.		N.W. Eagle I., W. Ireland	Longlines (200 m)	Rae and Wilson, 1952a: 107
X 51 3 cwts.		23' W.N.W. Black Rock, W. Ireland	Longlines (182 m)	
14 X 52	1 57	Hornbaek, Denmark		Nielsen, 1961, pers. comm., citing Danish press
7 X 56	1	Redcar, Yorks.	Found ashore dead	Wheeler, 1961, pers. comm.
24 X 45	1♀ 59	50' W.N.W. Heligoland	Cutter—comm.	Krefft, 1961, pers. comm.
27 X 48	1♀ 59	55°28'N., 1°25'E.	Trawler (70 m)	"
27 X 48	1♂ 54	55°28'N., 1°25'E.	Trawler (70 m)	"
12 X 49	1 61	Dogger Bank	Trawler	"
13 X 56	1♂ 56	N.W. Reef, W. Dogger Bank	Cutter	"
X 1850 4 (1 = 58)		Redcar, Yorks.	Stranded on beach	Rudd, 1850: 2971
7 X 54	1	about 1' S. of Bray Head, Valentia Is., Co. Kerry, Ireland	Trawling with mackerel spinners for baitfish; fell off line when being hauled in	Healy, 1955: 254
7 X 54	1 39.6 t.l.; 32 f.l.	about 1' S. of Bray Head, Valentia Is., Co. Kerry, Ireland	Trawl—mackerel lines and spinners for bait	"
7 X 54	1 42.6 t.l.; 34.7 f.l.	about 1' S. of Bray Head, Valentia Is., Co. Kerry, Ireland	Trawl—mackerel lines and spinners for bait	"
25 X 48	1 34.5 t.l.; 28 f.l.	Castletownsend Harbour, Co. Cork, Ireland	Motorboat	Gibson, 1949: 309
X–XI 1844 3		Redcar, Yorks.	Stranded	Rudd, 1845: 833
19 X 1895 61		near Scarborough, Yorks.	Caught	Clarke, 1895: 436; 1928: 109
29 X 1895 60		near Gt. Yarmouth, Norfolk	Taken in herringnets	Patterson, 1897: 548
6 X 1885 1	58 (extreme l.)	Redcar, Yorks.	Caught	Lofthouse, 1886: 640

Date	No.	Length	Locality	Notes	Reference
30 X 27	1	(large spec.)	Scalby Ness, nr. Scarborough, Yorks.	Stranded (mutilated by rats and gulls)	Clarke, 1928: 107
7 X 56	1		Redcar, Yorks.	Stranded	Wheeler, 1961, pers. comm.
2 X 58	2	40; 43	Porcupine Bank off S.W. Ireland	Trawl	Rae and Lamont, 1960: 78; 1962, pers. comm.
31 X 27	1	61 (extreme l.)	Scarborough South Bay, Yorks.	Stranded alive	Clarke, 1928: 107–8
9 X 22	1	59.5	Whitby, Yorks.	Stranded	Clarke, 1928: 109, citing Snowden, pers. comm.
1 X 34	1	30.5	near Scarborough, Yorks.	Taken from stomach of a cod	Clarke, 1935: 44
12 X 1892	1	60 t.l.	Hunstanton Beach, Norfolk	Stranded alive after gale	Le Strange, 1894: 421–2
30 X 1885	1		off Palling, Norfolk	Live caught?	Lowe, 1894: 636
X 1843	1		Tramore, Co. Waterford, Ireland		Thompson, 1856: 92, cited by Went, 1962; pers. comm.
31 X 61	1	57 t.l.; 48.2 f.l.; 43.7 s.l.	Wyk, Insel Föhr (off W. Germany)	Drifting inshore in half-dead condition—thrown ashore by a boy with his hands	Krefft, 1962: 15–17; 1962, pers. comm.
4 X 23	1		32' N. of Broad Haven, Co. Mayo, Ireland		Rae and Lamont, 1962, pers. comm.
6 X 24	1		45' W. × S. Black Rock		"
12 X 25	3		20' N.W. × W. of Eagle Island, Ireland		"
22 X 25	1		21' N.W. × W. of Eagle Island, Ireland		"
22 X 25	1		80' W. × N. of Tory Island, Ireland		"
4 X 26	3		20' N.W. of Eagle Island, Ireland		"
5 X 26	1		18' N.W. × W. of Eagle Island, Ireland		"
4 X 29	2♂ 1♀	60; 62 58.5	20' N.W. of Eagle Island, Ireland		"
28 X 47	1		N.W. of Eagle Is. to N. Rathlin	Longline	"
12 X 21	1	43 s.l.	Øresund, near Snidstrup, Denmark	Net (22 ft)	Jensen, 1940: 194
X 1896	1		Kolding Fjord, Denmark	Live caught	Otterström, 1912: 106
NOVEMBER					
3 XI 1894	1	32 s.l.	Faroes		Zoological Museum, Univ. of Copenhagen
16 XI 29	1		Blokhus, Denmark	Cod nets (3–5 fm)	Jensen, 1940: 195
17 XI 29	1		Vigsø Bugt, Denmark, near land	Cod nets (5 fm)	Jensen, 1940: 196

TABLE 2. *Continued*

Date	No. (and Sex)	Length (cm.)	Locality	Circumstances	Authority and Remarks
NI 49	1	56.5	Northern North Sea	Comm. landings	Krefft, 1961, pers. comm.
5 XI 27	1	60 t.l.	Lønstrup, Denmark	Live caught	Zoological Museum, Univ. of Copenhagen
16 XI 55	1	44.5 s.l.	Ved Kyndbyhavn ilsefljorden, Denmark	Live caught in bottom net (4 m)	"
14 XI 41	1		Gilleleje, Denmark	Stranded	Nielsen, 1961, pers. comm., citing Danish press
30 XI 51	1	54	West side of Eglohn W. Skelskør, Denmark	Pound net	Zoological Museum, Univ. of Copenhagen
4 XI 52	1		Esbjerghavn, Denmark	Stranded	Nielsen, 1961, pers. comm., citing Danish press
14 XI 49	1	61	57 50'N., 1 30'E.	Trawl	Krefft, 1961, pers. comm.
	1	59			
21 XI 49	1	44	Northern North Sea, Fladen ground	Trawl	"
22 XI 50	1/2 basket in 1 haul		Viking Bank at 60 N.	Trawl	"
4 XI 48	1	61	58 35'N., 2 10'E.	Caught (95 m)	Kristensen, 1950: 50
8 XI 48	1		from about same area as 58 N., 02'E.	Caught	"
16 XI 48	1	38.7	100' S.W. of Rockall	Longline	Rae and Lamont, 1962, pers. comm.
3 XI 49	1	46.4	30' E. of Fraserburgh	Seine net	"
9 XI 49	1		Queensferry, Firth of Forth	Stranded	"
11 XI 49	1	51	12' N.E. of Bell Rock	Trawl	"
14 XI 49	2	43.8; 48.7	18' N.N.W. of Flugga	Trawl	"
14 XI 49	2		N.W. of Flugga, Shetland	Trawl	"
14 XI 49	1♂	47	30' N. of Flugga, Shetland	Trawl	"
14 XI 49	4		20' N.N.W. of Ronasvoe, Shetland	Trawl	"
27 XI 49	1♀	57	180' N.E. 1/4 E. Buchanness	Trawl	"
28 XI 49			12' E. of Sule Skerry	Trawl	"
29 XI 49	2		145' N.E. × E. 1/2 E. of Buchanness	Trawl	"
9 XI 60	2♀	54.8; 53.8	Fair Isle–Foula	Trawl	"
20 XI 60	1	60	Rosemarkie Beach, Inverness Firth (Moray Firth)	Stranded	"
22 XI 60	1	57.2	Mid Minch	Drift net	"
25 XI 60	1♀	60.3	Aberdeen channel	Stranded	"
25 XI 60	1♀	60	4' E. of Tarbat Ness, Moray Firth	Seine net	"
28 XI 60	1♂	55.5	Dornoch Beach, Dornoch Firth, Sutherland	Stranded	"

Date	No.	Size	Locality	Method	Reference
30 XI 60	1	55	5' off St. Abbs Head, Berwick	Seine net	"
30 XI 60	1 ♂	58	8' E.N.E. of Lossiemouth, Moray Firth	Seine net	"
ca. 10 XI 61	1 ♀	57.5	off Cape Wrath	Trawl	"
13 XI 61	1 ♂	60.4	24' S.S.E. of Aberdeen	Trawl	"
26 XI 52	1 ♂	56.4	Burghead Bay, Moray Firth	Trawl	Rae and Wilson, 1953a: 147; 1953b: 138
29 XI 52	1		30–37' E.S.E. Aberdeen	Trawl	"
XI 55	1	51–63	58°20'N., 2°15'E.	Catch	Verwey, 1956: 96–7
XI 25	1		Hansted Fyr, Denmark	Commercial	Jensen, 1940: 194
24 XI 26	1		near Randers Fjord, Denmark		"
1 XI 27	1	61 t.l.	Aalbaek, Denmark	Stranded alive	Jensen, 1940: 195
2 XI 27	1		Lønstrup, Denmark	Stranded	"
3 XI 27	1		Tversted Forstrand, Denmark		"
4 XI 27	1		near Hanstholm, Denmark	(10 m)	"
6 XI 27	1		Odde, Mariager Fjord, 3 km. offshore, Denmark	Net (3 m)	"
15 XI 27	1		Febbersted, Denmark	Stranded	"
13 XI 27	1		Tisvildeleje, Denmark	Caught in very shallow water	"
14 XI 27	1		½' from Hansted, Denmark	Cod net	"
15 XI 27	1		N. Vorupør, Denmark	Stranded	"
18 XI 27	1		Hjembaek Strand, Djursland, Denmark		"
XI 27	1		Skagerak, ca. 1,000 m from land (off Skagen)	Caught	"
9 XI 29	1		Agger Tange, Denmark		Nilsson, 1855: 124
XI 1827	1		Skälderviken, Sweden		Nordgård, 1928: 63–4; Bernhoft-Osa, 1935: 101
15 XI 27	1 ♀	60	Sør-Froia, Trøndelag, Norway	Live caught	
2 XI 53	1 ♂	57	30' N.E. × N. Fraserburgh, Aberdeen	Trawl	Rae and Wilson, 1954a: 178
12 XI 53	1 ♂	56.5	5' S.E. Sule Skerry; 59°N., 4°20'W.	Trawl	
11 XI 27	1	59–60	Aberlady, E. Lothian	Washed ashore	Stephen, 1928: 28
17 XI 27	1	59–60	Firth of Forth	Caught	
11 XI 27	2	59–60	220' E.N.E. May Island	Caught	"
30 XI 33	1	58	North Berwick Beach, East Lothian	Stranded	Stephen, 1934: 27
5 XI 52	2		14' E.S.E. Sumburgh Head, Shetland	Trawl	Rae and Wilson, 1953a: 147; 1953b: 138
5 XI 52	2		110' N.E. × N. Buchanness, Aberdeen	Trawl	"
6 XI 52	1		Dunby Rock, Cruden Bay	Seine	"
7 XI 52	1	59	off Montrose, Angus	Seine	"
8 XI 52	1	54.6	N. of Peterhead, Aberdeen	Stranded	"

TABLE 2. *Continued*

DATE	NO. (AND SEX)	LENGTH (CMS.)	LOCALITY	CIRCUMSTANCES	AUTHORITY AND REMARKS
8 XI 52	1	55	Whitehills, Moray Firth	Stranded	"
9 XI 52	1	57.2	Harbour of Refuge, Peterhead	Stranded	"
11 XI 52	1♂	54	45' S. × E. Aberdeen	Trawl	"
13 XI 52	1♂	55.7	52' S. × E. Aberdeen	Trawl	"
14 XI 52	1♀	57.5	14' S.E. × E. Bell Rock	Trawl	"
14 XI 52	1♂	56.5	Old North Harbour, Peterhead	Stranded	"
18 XI 52	1		Granton Harbour, Firth of Forth	Stranded	"
18 XI 52	1♂	55	3' N.E. Tolsta Head, Lewis	Drift net	"
20 XI 52	1♀	55.5	10' N.N.W. Flugga, Shetland	Trawl	"
21 XI 52	1	54.6	Stronsay, Orkney	Stranded	"
21 XI 52	1♀	55.5	Fortrose, Ross, and Cromarty		Jensen, 1940: 196
25 XI 52	1♀	53.3	Burghead Harbour, Moray Firth	Stranded	Thompson, 1918: 63–64: + details, Rae and Lamont, 1962, pers. comm.
XI 29	1		Lild Strand, Denmark	Stranded	
22 XI 11	1		16' S.S.W. Fair Isle	Caught	
20 XI 12	1		5' S.E. Collieston, Aberdeen		Rae and Lamont, 1962, pers. comm.
25 XI 12	1		5' E. × N. 1½ N. Aberdeen		"
29 XI 12	1		5' E.N.E. Aberdeen		"
30 XI 12	1		7–8' S.E. Buchanness		"
30 XI 12	1		S.E. Buchanness		
3 XI 24	1		90' N.E. × N. of Buchanness, Aberdeen		
13 XI 24	1♂	60	off Burnmouth, Berwick		
3 XI 27	1♂	58.5	St. Combs, Moray Firth	Stranded	
14 XI 27	1♀	60	Montrose Basin, Angus		
15 XI 27	1♂	56	Shandwick Bay, Moray Firth		
17 XI 27	1♀	61	Aberdour, Firth of Forth		
21 XI 27	1		St. Combs, Moray Firth	Stranded	
25 XI 27	1		off Golspie, Moray Firth	Small line	
30 XI 27	1♂	62	Cruden Bay, Aberdeen	Gaffed	
22 XI 28	1		7–9' S.S.E. of Buchanness		
6 XI 29	1		35' N.E. × E. Outskerries, Shetland		
20 XI 34	1		195' N.E. × E. Aberdeen		
26 XI 34	1		25' S.E. of Samburgh Head, Shetland		
5 XI 35	1		140' N.E. ½ E. Buchanness		
2 XI 36	1		30' N.E. × E. Buchanness		

10 XI 36	1		30' E.N.E. Aberdeen		"
11 XI 36	1		14' S.E. × E. Noss Head, Caithness		"
11 XI 36	1		14' E.S.E. Noss Head, Caithness		"
26 XI 36	1♂	60	5' E. ½ N. of Bass Rock, Firth of Forth	Trawl	"
4 XI 37	1♀		Bervie Bay, Kincardine	Stranded	"
19 XI 37	1		18' E.S.E. Sumburgh Head, Shetland		
25 XI 38	1♀	59	Freswick, Caithness	Stranded	Rae and Lamont, 1960: 78
29 XI 58	1		Mar Bank, off E. Scotland	Trawl	Rae and Wilson, 1956a: 100
10 XI 55	1	55	30' N.N.E. Fraserburgh, Aberdeen	Trawl	
25 XI 1825	1	60.7 t.l.	Landskrona, Hildesborg, Sweden	Stranded after N.W. storm	Smitt *et al.*, 1893: 79; Schagerström, 1827: 207
5 XI 55	1♂	52.5 t.l.	15–18' E. Rattray Head, Aberdeen	Trawl	Rae and Wilson, 1956a: 100; 1957: 103
10 XI 55	1♂	55.0 t.l.	30' N.N.E. of Fraserburgh, Aberdeen	Trawl	Rae and Wilson, 1956a: 100; 1962, pers. comm.
12 XI 55	1♀	52 t.l.	Basta Voe, N. Yell, Shetland	Stranded	Rae and Wilson, 1956a: 100; 1957: 103
21 XI 55	1♀	55.3 t.l.	Hatson Beach, Orkney	Stranded (seen to "rush itself ashore")	"
22 XI 55	1	58.4 t.l.	Buchan Deeps	Trawl	"
26 XI 55	1		near Bell Rock, Inchcape	Trawl	
28 XI 55	1♀	53 t.l.	4' off Covesea, Moray Firth	Seine	Rae and Wilson, 1954b: 117; 1954a: 178
3 XI 53	1♂	47.5	St. Kilda	Trawl	Rae and Wilson, 1952a: 107; 1952b: 116
XI 51	1	53	14' N.W. Flugga, Shetland	Trawl	Rae and Wilson, 1952b: 116
XI 51	1		16' S.S.E. Todhead, Kincardine	Trawl	Rae and Lamont, 1959: 85; 1962, pers. comm.
9 XI 57	1♂	58.5	20' N.N.E. Fraserburgh, Aberdeen	Seine net	Rae and Lamont, 1959: 85; 1962, pers. comm.
3 XI 56	1	40	North Sea (58°66'N., 3°27'E.)	Caught	Kotthaus, 1958: 96
30 XI 57	1	52.1	8' S. of Todhead (Kincardine)	Trawl	Rae and Lamont, 1959: 85; 1962, pers. comm.
25 XI 57	1		Newburgh, Aberdeen	Stranded	
7 XI 56	1♀	62	9' E. ½ N. Rattray Head, Aberdeen	Trawl	Rae and Wilson, 1958b: 96; 1962, pers. comm.
7 XI 56	1		9' E. ½ N. Rattray Head, Aberdeen	Trawl	
12 XI 57	1	54	200" E.S.E. Aberdeen	Trawl	Rae and Lamont, 1959: 85; 1962, pers. comm.
14 XI 53	1		Portobello, Firth of Forth	Stranded	Rae and Wilson, 1954b: 117; 1954a: 178
14 XI 56	1	56.6	Montrose Bay, Aberdeen	Cod net	Rae and Wilson, 1958b: 96; 1962, pers. comm.
XI 56	1		Tain, Moray Firth	Stranded	"

TABLE 2. *Continued*

DATE	No. (AND SEX)	LENGTH (CMS.)	LOCALITY	CIRCUMSTANCES	AUTHORITY AND REMARKS
XI 17	1		Ardmore, Co. Waterford, Ireland	Washed ashore	Went, 1962, pers. comm.
XI 09	1		Loughal, Ireland	Washed ashore alive	"
9 XI 1895	1		Between Whitby and East Row, Yorks.	Stranded on beach	Stephenson, 1896: 239
14 XI 1893	1		Whitby, Yorks.	Washed up on the sands	Stephenson, 1894: 211
3 XI 27	1		Scarborough South Bay, Yorks.	Washed ashore dead	Clarke, 1928: 108
5 XI 27	1	62	Scarborough Harbour, Yorks.	Stranded alive	"
7 XI 27	1	62	Scarborough Harbour, Yorks.	Stranded alive	"
7 XI 27	1		Scarborough, Yorks.	Taken on the sands	"
12 XI 27	1	59	Scarborough, Yorks.	Stranded alive	"
16 XI 27	1		Scarborough South Sands	Washed ashore—dead and decomposed	"
16 XI 27	1	58.4	near Bathing Pool, Scarborough, Yorks.	Stranded alive	"
17 XI 27	1	60.4	Carnelian Bay, 2' S. of Scarborough, Yorks.	Stranded alive	"
24 XI 27	1		Scarborough South Bay, Yorks.	Washed ashore dead	"
28 XI 27	1	57.2	Scarborough South Sands, Yorks.	Washed ashore dead, but quite fresh	"
4 XI 27	2		Filey, Yorks.	Stranded	"
9 XI 27	1		Filey, Yorks.	Stranded	"
6 XI 27	1		Upgang, near Whitby, Yorks.	Stranded	"
16 XI 27	1		Whitby, Yorks.	Stranded	"
XI 27	1		Runswick, Yorks.	Stranded	"
29 XI 21	1		Whitby, Yorks.	Captured in shallow water on the sands	Clarke, 1928: 109, citing Snowden, pers. comm.
17 XI 25	1	46	Filey, Yorks.	Caught on a fisherman's hook baited with a Dahlia anemone	Clarke, 1928: 109
4 XI 27	1	58.4	Withernsea, Yorks.	Washed up on the shore	Sheppard, 1928: 25
XI 24	1	66	South Sands, Bridlington, Yorks.	Washed ashore alive	Sheppard, 1925: 53–4
XI 1799	1	41	In the inlet that runs up to Kingsbridge, S. coast of Devon	Taken alive—left by the tide	Montagu, 1804: 293
XI 55	2	51–63	Zeeland, Holland	Catch	Verwey, 1956: 96–97
XI 55	1	51–63	54°25'N., 2°25'E.	Catch	"
XI 52	3	51–60	Texel Hole oyster grounds, Holland	Catch	Verwey, 1953: 346–7
XI 52	6	51–60	Dutch coast, near Haarlem, Holland	Stranded	"
XI 57	1	56	Wijk aan Zee, Holland	Stranded	Verwey, 1960a: 548–9

Date	No.	Size	Locality	Capture	Reference
XI 58	1 ♀	53	Callantsoog, Holland	Stranded	Verwey, 1960b: 564–5
13 XI 22	1	46 s.l.	Northeast coast of Romsø, Denmark	Stranded	Jensen, 1940: 194
XI 22	1		Svenborg Sund, Denmark	Cod trap	Jensen, 1940: 194, citing Dansk Fiskeritidende, 1922: 480
12 XI 1806	1	84	Swansea Bay, Wales	Alive on shore	Turton, 1807: 98
25 XI 60	1	58.5	Thorpness, Suffolk		Wheeler, 1961, pers. comm., citing "Angling Times," 25 XI 60
2 XI 50	1 ♂	56.5	Dogger Bank	Trawl	Krefft, 1961, pers. comm.
15 XI 48	1	39.4 t.l.; 29.8 f.l.	5′ S. of Slea Head, Co. Kerry, Ireland	Drift-net fishing for mackerel	Gibson, 1949: 309
10 XI 1850	1		Redcar, Yorks.	Stranded	Rudd, 1851: 3010
13 XI 1890	1		Mount's Bay near Penzance, Cornwall	Caught with hook and line	Cornish, 1891: 35
23 XI 1894	1	64	Caister, Norfolk	Toppled ashore during heavy wind	Patterson, 1897: 548
9 XI 1821	1	"full-sized"	Cromer beach, Norfolk	Found after a storm	Gurney, J. H., 1874: 19, citing Anna Gurney, 1821, MSS
XI 27	5		Norfolk coast, around Cromer	Caught	Grimpe, 1929: 163, citing Ehrenbaum, 1928: 709

DECEMBER

Date	No.	Size	Locality	Capture	Reference
3 XII 51	1		Berudeep, Iceland	Comm. landings	Brandes, Kotthaus and Krefft, 1953: 47
26 XII 15	1	64 t.l.	S. coast Iceland, off Snaefellsnes	Caught living (trawl?)	Saemundsson, 1922: 180
21 XII 50	1	50 t.l.	West-Tampen, Norway	Caught by porbeagle line (180 m)	Willgohs, 1954: 4
27 XII 55	1	53.3	Crail, Fife	Stranded	Rae and Wilson, 1956a: 100
XII 51	2		near Kirkaldy, Firth of Forth	Stranded	Rae and Wilson, 1952a: 107
XII 51	1		North Berwick, Firth of Forth	Stranded	″
1 XII 52	1		3′ S. Golspie, Moray Firth	Stranded	Rae and Wilson, 1953a: 147; 1953b: 138
3 XII 52	1		off Montrose, Angus	Seine	″
6 XII 52	1		12′ S.E. Aberdeen	Trawl	″
9 XII 52	1 ♀	58	15′ N.E. Longstone (S.E. Scotland)	Trawl	Rae and Wilson, 1953a: 147, citing "Fishing News," 1952: 147
XII 52	4		Whitley Bay, Yorks.	Washed ashore	Willgohs, 1954: 4
13 XII 51	1	54	Herdla, Hordaland, Norway	Drifting half-dead at the surface	″
XII 51	1		Hvaler, Østfjord, Norway	Half-dead on shore	″

TABLE 2. *Continued*

Date	No. (and Sex)	Length (cms)	Locality	Circumstances	Authority and Remarks
13 XII 21	1		near Hurup, Østjylland, Denmark	Net caught	Jensen, 1940: 194, citing Dansk Fiskeritidende, 1921: 508
4 XII 52	4	49; 3 × 52.5	50 km. W. of Shetland	"Fishing-line"	Willgohs, 1954: 4
10 XII 57	1 ♂	60	180′ E.N.E. Aberdeen	Trawl	Rae and Lamont, 1959: 85; 1961, pers. comm.
11 XII 57	1	50.8	Macduff, Moray Firth	Stranded	"
12 XII 57	1		off Johnshaven, Moray Firth	Stranded	"
16 XII 57	1	54.6	off Johnshaven, Moray Firth	Cod net	"
1 XII 55	2♀	56.5	Cranton Harbour, Firth of Forth	Gaffed	Rae and Wilson, 1956a: 100; 1957: 103
4 XII 55	3		Portobello, Firth of Forth	Stranded	"
21 XII 55	1	50.8	26′ E.S.E. Aberdeen	Trawl	Rae and Wilson, 1952b: 116; 1952a: 107
XII 51	1		47′ ½ E. Aberdeen	Trawl	"
XII 51	2		135′ N.E. × E. ½ E. from Aberdeen	Trawl	
6 XII 56	1		Inverness Firth (Moray Firth)	Drift net	Rae and Wilson, 1958b: 96; pers. comm.
29 XII 54	1♀	56.4	Gardenstown, Moray Firth	Stranded	Rae and Wilson, 1956b: 69
5 XII 56	1♀	52.5	8′ E. × N. of Rattray Head	Trawl	Rae and Wilson, 1958b: 96; pers. comm.
1 XII 58	1	52.0	Loch Carron, W. Ross.		Rae and Lamont, 1960: 78
16 XII 1843	1	47.2 f.l.	Tjörn, Göteborg (Bohuslän), Sweden	Cast up after N.W. storm	Smitt et al., 1893: 79
28 XII 27	1	57 t.l.	Sandnesfjord, Rogaland, Norway	Live caught—net (30 fm)	Schaanning, 1929: 1; Bernhoft-Osa, 1935: 101
XI–XII 1850	several		Firth of Forth, near Edinburgh	Washed ashore	Logan, 1851: 3058
22 XII 53	1♀	55	24′ S.S.E. Aberdeen	Trawl	Rae and Wilson, 1954b: 117; 1954a: 178
5 XII 28	1		As Vig, S. Horsensfjord, Denmark	Stranded	Jensen, 1940: 195
6 XII 34	1		Aalsgaarde, Denmark	Stranded alive	Jensen, 1940: citing Aage Jensen, 1937: 16
3 XII 1876	1	44 s.l.	Skagen, Denmark	Stranded after storm	J. Nielsen, 1961, pers. comm.
3 XII 51	1		Uggerby, N. Jutland, Denmark	Stranded after storm	"
5 XII 51	2	40; 25	Lonstrup, Denmark		Nielsen, 1961, pers. comm., citing Danish press
5 XII 51	several		Hirtshalls, Denmark	Stranded	"
6 XII 51	1	50	near Liseleje, Denmark	Stranded	"
5 XII 51	1		Skalderviken, Denmark		"
XII 52	1		Rørvig (W. Lyngkroen), Denmark	Stranded	"
11 XII 58	1		Kirkholmbugten by Juelsminde, Denmark	Shot by a hunter	"

19 XII 49	1	45	Kattegat; N. entrance of Øresund	Cutter	Krefft, 1961, pers. comm.
25 XII 51	1		7' N.E. Fehmarn, Baltic		Krefft, 1961, pers. comm., citing German press
6 XII 51	1		near Hundested, Denmark	Stranded	Nielsen, 1961, pers. comm., citing Danish press
XII 51	1	57	Sassnitz, Rügen, Baltic		Krefft, 1961, pers. comm.
16 XII 27	1	61	Jubilee Bank, S. Skagerak	Caught (24–34 m)	Grimpe, 1929: 163
7 XII 27	1		Vikhög—coast of Schonens, W. Øresund, Sweden	Caught	
1 XII 25	1		180' E.N.E. Aberdeen	Cod net	Rae and Lamont, 1962; pers. comm.
1 XII 56	1	52	Montrose Bay, Angus	Trawl	Rae and Wilson, 1958b: 96; pers. comm.
7 XII 56	1♂	57	Bell Rock		"
8 XII 56	2		Buddon Ness, Angus	Stranded	"
11 XII 50	1		Eday, Orkney	Stranded	Rae and Wilson, 1951: 83; pers. comm.
12 XII 27	2		vicinity of Cromarty, Moray Firth	Stranded	Rae and Lamont, 1962, pers. comm.
13 XII 27	2		St. Combs, Moray Firth	Stranded	"
20 XII 27	1		vicinity of Balintore, Moray Firth	Stranded	"
7 XII 36	1		20' S.E. × S. of Bard Head, Shetland		"
2 XII 38	1♀	57	Aberdeen Harbour		"
8 XII 38	1		40–55' E.N.E. of Aberdeen		"
9 XII 49	1		5' S.E. Red Head, Angus	Trawl	"
20 XII 49	1		near Dunbar, E. Lothian	Stranded	"
12 XII 08	1		16' N. × E. Rattray Head, Aberdeen	Stranded	Thompson, 1918: 63–64; + details, Rae and Lamont, 1962, pers. comm.
17 XII 08	1		160' N.E. ½ E. from Buchanness, Aberdeen		"
3 XII 09	2		180' E. × S. Aberdeen		"
20 XII 09	1		175'–180' E. × N. ¾ N., Aberdeen		"
8 XII 10	3		4' E. × N. Aberdeen		"
16 XII 10	1		5' E.S.E. Tod Head, Kincardine		"
31 XII 10	1		5' E.N.E. Aberdeen		"
29 XII 11	1		45' N. × W. Rattray Head, Aberdeen		"
3 XII 12			7' E.S.E. Buchanness, Aberdeen		"
10 XII 49	1♀	57	Texel, Holland	Stranded alive	Kristensen, 1950: 50
27 XII 49	1		Terschelling, Holland	Stranded	"
29 XII 49	1	53	Terschelling, Holland	Stranded	"
29 XII 49	1	40	near Bloemendaal, Holland	Stranded	"
29 XII 49	1♂	58	near Egmond, Holland	Stranded alive	"
2 XII 27	1	58.5	Scarborough, Yorks.	Stranded	Clarke, 1928: 108

TABLE 2. *Continued*

Date	No. (and Sex)	Length (cms)	Locality	Circumstances	Authority and Remarks
4 XII 27	1	57.2	Scarborough South Bay, Yorks.	Washed ashore dead and decomposed	"
10 XII 27	1	48.3	Scalby Ness, 2' S. of Scarborough, Yorks.	Washed ashore dead and decomposed	"
2 XII 27	1	62.2	Filey, near Scarborough, Yorks.	Stranded	"
XII 49	1		Whitby, Yorks.	Stranded	Rae and Wilson, 1951: 83, citing "Fishing News" of 10 Dec., 1949
20 XII 59	1 ♂	57	Farne Is., Northumberland	Stranded	Rae and Lamont, 1961: 105; pers. comm.
XII 1850	1		Lowestoft, Suffolk	Washed ashore	Gurney, 1851: 3058
XII 55	1	51–63	Zandvoort, Holland		Verwey, 1956: 96–7
XII 55	1	51–63	Zeeland, Holland		"
XII 55	1	51–63	Huisduinen, Holland		"
XII 52	3	51–60	Texel Hole oyster grounds, Holland	Catch	Verwey, 1953: 346–7
XII 52	7	51–60	Dutch coast, near Haarlem	Stranded	"
XII 56	3	50: 2 × 45	between Katwijk and Texel, Holland	Stranded	Verwey, 1958: 542–3
XII 56	1	53	off Callantsoog, Holland	Catch (9 m)	"
XII 57	2	56	Egmond, Holland	Stranded (1 ft)	Verwey, 1960a: 548–9
7 XII 27	1		Spodsbjerg Light	Stranded	Jensen, 1940: 195
28 XII 27	1	"About the usual size"	Whitby, Yorks.	Stranded	Clarke, 1928: 108
2 XII 22	1	58.5	Whitby, Yorks.	Stranded	Clarke, 1928: 109, citing Snowden, pers. comm.
XII 25	1		Filey, Yorks.	Caught with a line baited with a Dahlia Wartlet anemone	Stevenson, 1926: 26

NO SEASONAL INFORMATION

Date	No. (and Sex)	Length (cms)	Locality	Circumstances	Authority and Remarks
Nov. Dec. 1925	several		Bohuslän, Sweden The Skaw, Denmark	Stranded	Jensen, 1937: 16
1830	1		Kullen, Sweden (56°18'N., 12°28'E.)		Nilsson, 1855: 124
1850	1		Bohuslän, Sweden		"
before 1850	1	44.1 t.l.	vicinity of Bergen		Collett, 1902: 44

Date	No.	Size	Locality	Notes	Reference
1825	1		Gardenston Harbour, Gamrie, Banffshire	Left in hollow in rocks by the tide—behind the present (*i.e.* 1851) quay	Harris, 1851: 3302
1924	1		Skrea, Hallands Väderö I., Sweden	Live caught (trawl)	Goode, 1884: 335
?	1	54 t.l.	Skovshoved (on the Sound, *ca.* 10′ N. Copenhagen)	Live caught	Nielsen, 1961, pers. comm.
1851–52 (winter)	4		Redcar, Yorks.	Stranded	Rudd, 1852: 3504
1880	1		Grand Bank, Newfoundland	Live caught (trawl)	Goode, 1884: 335
1888	1		S. coast of Ireland		Went, 1962, pers. comm.
Nov./Dec. 1925 (prob. Aug.)	several		Øresund, Denmark	Stranded	Jensen, 1937: 16

Evolution of the Tapiroid Skeleton from *Heptodon* to *Tapirus*

by LEONARD B. RADINSKY

EVOLUTION OF THE TAPIROID SKELETON FROM
HEPTODON TO *TAPIRUS*

LEONARD B. RADINSKY[1]

INTRODUCTION

The purpose of this study is two-fold: first, to describe and illustrate the best-preserved known skeleton of an early Eocene perissodactyl and, second, to investigate the morphological changes which occurred during about 50 million years of evolution from the late early Eocene tapiroid *Heptodon* to the recent genus *Tapirus*.

Although equoid and tapiroid remains are fairly common in early Eocene deposits, good skeletons of these or other early Eocene perissodactyls are discouragingly rare. Most of the skeletal elements which have been found are incomplete, crushed, or coated with a hard deposit which makes preparation difficult. For these reasons no well-documented description of the osteology of an early Eocene perissodactyl has heretofore been published. The most detailed previous study, Kitts' revision of *Hyracotherium* (1956), is inadequately illustrated. The present paper therefore should fill a critical gap in knowledge of perissodactyl evolution.

This study is based on an almost complete, well preserved, and excellently prepared skeleton of *Heptodon posticus*, an early Eocene helaletid tapiroid. All early Eocene perissodactyls appear to have been extremely similar in skeletal morphology, with the main differences between the major groups expressed in the dentition. The osteological differences which do exist apparently reflect relatively small differences in size and do not appear to have phylogenetic significance. Therefore, the skeleton of *Heptodon* described below represents, probably fairly closely, the ancestral morphology not only of all later tapiroids, but of all other perissodactyls as well. To facilitate future studies by workers to whom the original material is not readily available, the bones described here are illustrated with figures drawn from several views.

Heptodon probably was directly ancestral to the modern tapirs, as well as to several extinct tapiroid lineages (see Radinsky, 1963a). In the following description comparisons are made between the skeleton of *Heptodon* and that of a modern species of *Tapirus*, *T. pinchaque*, to determine the extent of the osteological changes which occurred in this most conservative of surviving perissodactyl lineages. To aid interpretation of the functional significance of the observed changes, reference was made to Bressou, 1961, and to Campbell, 1936 and 1945, the most recent accounts of the myology of Recent species of *Tapirus*. In addition, I dissected the facial and fore limb musculature of a specimen of *Tapirus indicus*. My own observations and the published accounts confirm Gregory's (1929) restoration of the relatively unspecialized

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[1] Department of Biology, Brooklyn College, Brooklyn, N. Y., and Department of Vertebrate Paleontology, the American Museum of Natural History, New York.

musculature of a titanothere. Gregory's work is still the best one to consult for illustrations of muscle origins and insertions on the perissodactyl skeleton.

The skeleton of *Heptodon posticus* here described, MCZ 17670,[2] was collected in Lostcabinian (late Wasatchian) beds in the Wind River basin, Wyoming, by Mr. Henry Seton, who published a preliminary note on the specimen in 1931. Mr. Seton has generously allowed me to complete the description. The scientific value of MCZ 17670 has been greatly enhanced by Seton's skill and painstaking work in preparing it. Postcranial remains of *Heptodon* are known in only one other specimen, AMNH 294, an incomplete skeleton of *H. calciculus*. This was briefly described by Osborn and Wortman (1892), and differs from *H. posticus* primarily in its smaller size and more slender build. The systematics of *Heptodon* have been discussed in a recent revision of North American tapiroids (Radinsky, 1963a).

Of the four living species of *Tapirus, T. pinchaque* was chosen for comparison with *Heptodon* mainly because it is the least specialized of the surviving tapirs, and also because it is the rarest and least well known of the four species. Illustrations of its postcranial skeleton are published for the first time in this paper. Specimens of *Tapirus pinchaque* examined for this study include: MCZ:M 6037, YPM 204, and AMNH:M 149331 and 149424.

For knowledge of intermediate stages between *Heptodon* and *Tapirus*, comparisons were made with *Protapirus*, a primitive Oligocene tapirid. Although known species of *Protapirus* occur too late in time to be directly ancestral to later tapirids (see Schaub, 1928, p. 13), the genus is probably

representative of a morphological stage through which the main line of tapirid evolution passed. Of the skeleton of *Protapirus*, only the skull, atlas, fore limb (PU 10899), and manus (AMNH 662) are known. These were originally described by Hatcher (1896), and Wortman and Earle (1893), respectively, and were most recently redescribed by Scott (1941).

To avoid repetition in the comparisons of bones of *Heptodon* and *Tapirus*, differences in size will not be mentioned. These may be calculated from the illustrations. It will suffice to note here that *Heptodon posticus* is about 40 per cent smaller than *Tapirus pinchaque*.

I am extremely grateful to Mr. Henry Seton, whose encouragement and generous support made this paper possible. I wish to thank Professors B. Patterson and A. S. Romer for making available to me the resources of the Division of Vertebrate Paleontology of the Museum of Comparative Zoology, Miss B. Lawrence and Mr. C. Mack for facilitating my studies of recent tapirs in the Division of Mammalogy of the Museum of Comparative Zoology, and Dr. R. Van Gelder for permission to study tapir skeletons in the collections of the Department of Mammology of the American Museum of Natural History. The drawings of *Heptodon* limb bones are the excellent work of Mr. N. Strekalovski. The plates were drawn by Llewellyn I. Price. This study was supported by National Science Foundation Grant No. GB 2386.

OSTEOLOGY

Skull and Mandible

The skull of *Heptodon posticus* included in MCZ 17670 is one of the best-preserved early Eocene perissodactyl skulls ever discovered (see Pls. 1–3). A slight anterior displacement of the right side of the skull, and a crushing of the right side of the rostrum, which resulted in a slight dorsal displacement of the right nasal bone, are the only evident distortions in proportions.

Fig. 1. Skull and mandible. Above, *Heptodon posticus*, MCZ 17670, × ½. Below, *Tapirus pinchaque*, YPM 204 (after Hatcher, 1896, pl. 5), × ¼.

The skull (see Fig. 1 and Pls. 1–3) is relatively long and narrow, measuring 195 mm from the anterior tip of the premaxilla to the dorsal edge of the foramen magnum, and about 80 mm wide across the zygomatic arches. The occiput is 56 mm high (from basioccipital to top of nuchal crest) and has a maximum width of 46 mm (across the post-tympanic processes). The preorbital portion of the skull is slightly longer than the postorbital portion. The nasal incision extends back to a point over the postcanine diastema, closer to P^1 than C^1. The premaxillae contact the nasals dorsally and ex- clude the maxillae from the nasal incision. The infraorbital foramen is located above the front of P^3 and the anterior edge of the orbit is above the anterior border of M^2. The lacrimal has a relatively small facial portion, and bears a triangular tubercle on the rim of the orbit. The supraorbital proc- esses are relatively massive and are followed by a pronounced postorbital constriction. The braincase is slightly expanded and the sagittal and lambdoidal crests are promi- nent. The zygomatic arches are relatively slender. The external auditory meatus is widely open ventrally; it is bounded ante-

riorly by a relatively prominent postglenoid process and posteriorly by a short, antero-ventrally projecting post-tympanic process. The paroccipital process is relatively long and thin, slightly flattened anteroposteriorly, and extends posteroventrally and slightly laterally.

The palate is almost flat from front to back and only slightly arched transversely. It has a pair of small elongate incisive foramina between the third incisors, and a long deep anterior median groove which may have opened into the nasal passage. The internal nares open at the posterior border of M^2. The interpterygoid fossa is relatively deep and narrow, with no trace of a vomer on the presphenoid almost as far forward as the anterior border of the choanae. The glenoid fossa is relatively flat. It is bounded posteriorly by a strong post-

glenoid process which is oriented postero-laterally at an angle of about 30 degrees from the long axis of the skull. The basi-cranial axis is inclined slightly anterodor-sally relative to the plane of the palate.

At the anterior edge of the orbit (see Fig. 2) the lacrimal bone is too broken to allow accurate determination of the number or configuration of the openings into the nasolacrimal canal. The maxillary foramen is visible in the extreme anteroventral corner of the orbit. The sphenopalatine foramen is located above the anterior edge of M^3, and is relatively large; a small posterior palatine foramen is located posteroventral to the sphenopalatine foramen. Sutures between the bones of the orbit cannot be definitely determined, partly due to the advanced age of MCZ 17670 (the teeth are heavily worn), and partly because the bones are extensively fractured.

The posterior part of the medial wall of the orbit (see Fig. 2) is pierced by four foramina, arranged in a posteroventrally descending row. Beginning with the most anterior one, which is located a short distance behind the posterior palatine foramen, these are: a small ethmoid foramen, a very large optic foramen, a smaller, vertically-bilobed, slit-like, anterior lacerate foramen (= orbital fissure or sphenoidal foramen), and the anterior opening of the alisphenoid canal. Examination of the interior of the braincase revealed a small foramen, apparently the foramen rotundum, opening into the alisphenoid canal. The optic foramen is unusually large and Simpson (1952, p. 200) suggested that the equally large, apparently homologous foramen in *Hyracotherium* was the confluent opening of the optic and anterior lacerate foramina. However, inside the braincase of *Heptodon* it can be seen that the left and right internal openings of the large foramen in question are confined entirely within the bounds of the optic chiasma and there are no grooves suggesting that nerves other than the optic left through the foramen. The presence of

Fig. 2. *Heptodon posticus*. MCZ 17670. Above, lateral view of orbital region with zygomatic arch removed. Below, anterolateral view of same region. × ½. For abbreviations see p. 102.

a foramen opening into the alisphenoid canal confirms the interpretation that the slit-like opening behind the optic foramen is the anterior lacerate foramen.

Above and slightly posterior to the anterior lacerate foramen on each side of the skull is an irregularly-shaped opening, at least part of which is artificial, but which may include a natural opening into the braincase (presumably the sinus canal foramen). There is a pit immediately above the anterior opening of the alisphenoid canal. A shallow vertical groove which ascends

Fig. 3. *Heptodon posticus.* MCZ 17670. Left, restoration of basicranial region of skull. Right, ventrolateral view of restored left petrosal, with tympanic and tegmen tympani removed. × ½.

from the laterodorsal border of the anterior opening of the alisphenoid canal may mark the course of the supraorbital artery, or possibly the deep temporal artery.

The foramen ovale (see Fig. 3) is separated from the middle lacerate foramen by a strip of alisphenoid about 7.5 mm wide,

the posterior border of which is notched by two grooves. The more lateral of the two, located just medial to the anterior edge of the postglenoid process, is relatively broad and probably marks the passage of the internal maxillary artery. The second, more medial groove, is narrow and slit-like, and probably contained the chorda tympani. The postglenoid foramen is relatively large. In ventral view the basisphenoid overlaps the ventral border of the petrosal. There is a medium-sized posterior lacerate foramen, a relatively large hypoglossal (or condyloid) foramen, and a medium-sized mastoid foramen.

Both petrosals of MCZ 17670 lack small portions, but fortunately the missing parts of each petrosal are preserved on the opposite side so that it is possible to obtain a composite picture of the entire bone (see Fig. 3). The ventral border of the petrosal is relatively long and convex, and the anterior border is relatively short and concave. Seen in ventrolateral view, the surface of the petrosal is flat anteroventrally, and swells posterodorsally towards a relatively low promontorium. The surface of the promontorium is smooth, and shows no traces of grooves for blood vessels. The tegmen tympani extends relatively far ventrally, forming the lateral wall of a deep groove for the facial nerve. This is similar to the condition in modern tapirs in which the facial nerve runs posteriorly along the lateral face of the petrosal in a ventrally-open groove, rather than in an enclosed canal. Two small foramina are present on the lateral face of the tegmen tympani. The lower and slightly more medial one probably is the facial hiatus, and thus served for the exit of the great superficial petrosal nerve (which joins the great deep petrosal nerve anteriorly to form the vidian nerve). The higher and more laterally situated foramen may have transmitted the small superficial petrosal nerve.

The tegmen tympani is broken off above the level of the facial canal on the right

petrosal, exposing the opening of the facial canal and the fenestra ovalis. The latter is located posteriorly and slightly ventrally from the former. A very small foramen, possibly a nutrient foramen, is present on both petrosals a short distance anteroventral to the fenestra ovalis. The fenestra rotunda is located a short distance posteroventral to the fenestra ovalis. A deep V-shaped groove extends posteroventrally from the fenestra rotunda and separates the main body of the petrosal from a small, globose posterior portion. This groove occupies approximately the same position as the auricular branch of the vagus nerve (which joins the facial nerve near the stylomastoid foramen), but appears too large to have housed that nerve alone.

The stylomastoid foramen is represented by a broadly open groove anteromedial to the post-tympanic process. No tympanohyal is preserved; the broken surface anterior to the stylomastoid foramen on left and right petrosals suggests that one may originally have been present. There are no separate fossae for the stapedius or tensor tympani muscles. These presumably occupied the same groove as the facial nerve, the tensor tympani at the anterior end of the groove, lateral to the facial nerve, and the stapedius at the posterior end, medial to the nerve.

On the medial side of the petrosal a shallow depression adjacent to the concavity of the anterior edge may have accommodated the semilunar (Gasserian) ganglion of the trigeminal nerve. The internal auditory meatus is relatively large and elongate in an almost vertical direction. Cochlear and vestibular aqueducts are visible near the posterior edge of the petrosal, the former posteroventral and the latter posterodorsal to the internal auditory meatus.

The entire tympanic bone was preserved on the left side but was largely destroyed during the preparation of a latex mold of the skull. Fortunately, photographs and drawings made by Henry Seton prior to this mishap provide a record of the config-

uration of this bone. The tympanic in this early Eocene tapiroid is a semicircular strip of bone, dorsoventrally flattened and slightly expanded in a horizontal plane. In other words, it is only slightly modified from the simple, narrow, open tympanic ring which is considered primitive for mammals. Kitts (1956, p. 17) stated that the early Eocene equoid *Hyracotherium* had a tympanic bulla which was ". . . apparently oval in shape and moderately inflated." Re-examination of the specimens involved showed that Kitts mistook the petrosal for a tympanic bulla. Except for the skull of *Heptodon posticus* described here, I know of no other specimen of an early Eocene perissodactyl in which the tympanic is preserved. The tympanic probably was a relatively narrow semicircular strip of bone in all early Eocene perissodactyls. Its failure to be preserved in otherwise complete skulls is probably because it was loosely attached to the skull, as in modern tapirs.

Portions of at least some of the auditory ossicles are visible dorsal and medial to the tympanic ring, but are too fragile to be removed from the last remnants of the hard sandstone matrix. Their description must await discovery of additional specimens.

The symphysis is slightly constricted and extends back as far as P_1. Its dorsal surface is deeply concave transversely. Three small mental foramina are visible, beneath C_1, the middle of the diastema, and P_2. The body of the mandible is relatively long and slender, with a very slightly convex ventral border. The angle is moderately convex and extends relatively far behind the condyle and slightly below the ventral border of the body. The condyle is located relatively high above the tooth row and is inclined medioventrally at an angle of about 20 degrees from horizontal. Its articular surface slopes anteriorly and a small facet continues ventrally onto the medial third of the posterior face of the condyle. The coronoid process is relatively small and vertical. On the lateral surface of the ascending

ramus a pronounced fossa for the zygomaticomandibularis extends ventrally to about the level of the tooth row. The border of the insertion area of the masseter is marked by a fairly prominent ridge for most of its length. The medial surface of the angle is slightly concave and bears prominent scars from the insertion of the internal pterygoid.

COMPARISON WITH TAPIRUS

The skull of *Tapirus pinchaque* (see Fig. 1) differs from that of *Heptodon* in several features, most of which are related to one or more of three basic developments: evolution of a proboscis, relative enlargement and change in proportions of the brain, and increased specialization of the masticatory apparatus.

The most obvious differences between the skulls of *Heptodon* and *Tapirus* are those associated with proboscis development. Primary modifications for the proboscis are the enlargement (or retraction) of the nasal incision, which provides room for the main mass of the proboscis, and shortening of the nasals, to allow flexibility to that organ. The nasal incision in *Tapirus* extends back over the orbits, and the nasals do not reach beyond the first premolar. An additional factor which adds to the vertical dimension of the nasal incision in *Tapirus* is the higher position of the nasals in that genus, which results from the presence of a frontal sinus. Frontal sinus development is correlated with changes in brain proportions, and will be discussed below. The nasal diverticulum (a blind cartilaginous sac which opens into the main nasal passage) has been displaced from the nasal incision in *Tapirus* and is lodged in a long, broad groove which begins on the ascending process of the maxilla, extends up along the posterior border of the incision on the anterior edge of the frontals, and terminates in a curl on the posterior edge of the nasals. The absence of a groove or fossa for the nasal diverticulum in *Heptodon* indicates that the diverticulum in that primitive tapiroid must have been relatively small and lodged in the nasal incision, as in modern horses and rhinos.

Secondary cranial modifications associated with proboscis development in *Tapirus* include a posterior displacement of the nasal cavity, strengthening of the premaxillae, and possibly the anterior shift of the orbit. In *Heptodon* the nasal cavity is located in front of the orbit, with the cribriform plate situated near the anterior border of the frontals, at the anterior edge of the orbit. In *Tapirus*, the tremendous expansion of the nasal incision has removed most of the lateral walls of the rostrum, and the greater part of the chamber which houses the ethmoturbinals is located *between* the orbits, with the cribriform plate located well behind the orbit, near the posterior border of the frontals. This has resulted in a lateral displacement of the walls of the orbit which obliterates the postorbital constriction and greatly deaccentuates the supraorbital processes. Another result of the posterior displacement of the nasal chamber relative to the orbits is that the internal nares, which open posteriorly in *Heptodon*, open downward as well as backward in *Tapirus*.

The expansion of the nasal incision in *Tapirus* has left the premaxillae extending far out, relatively unsupported. Presumably to strengthen this area against the vertical stresses which result from use of the incisors, the premaxillae are thickened and arch downward and, with the anterior ends of the maxillae, are closer together, forming a relatively deep, narrow, and arched projection on which the incisors and canines are borne. Associated with this development, the two lateral incisive foramina seen in *Heptodon* are merged into a single, large, median opening in *Tapirus*, extending back almost to the first premolar. The large size of this opening is probably related to the fact that it occupies that part of the palate least involved in transmitting vertical stresses from the incisors and canines, and

thus needs no bony support. Another factor possibly related to the strengthening of the premaxillae in *Tapirus* is the large size of the third incisor, which has been transformed into a small tusk which occludes against the front of the large lower canine. The upper third incisor of *Tapirus* is located more anteriorly than its functional counterpart, the upper canine, is in *Heptodon*, and would require stronger premaxillae for support.

The orbit is located more anteriorly in *Tapirus* than in *Heptodon*. This may be advantageous for operation of the proboscis since the main muscles involved (the levator nasolabialis and superior and inferior maxillolabialis) take origin on the anterior rim of the orbit and it would be mechanically more advantageous to have them originate nearer to their insertions. Another result of the anterior displacement of the orbit in *Tapirus* is that it brings the masseter forward over a greater portion of the tooth row, which increases the mechanical advantage of that muscle in mastication (see discussion below).

The skull is larger and heavier relative to the body in the modern tapir than in *Heptodon*. Probably reflecting this difference, the paroccipital process is relatively more robust, and is vertically oriented and fused to the post-tympanic process, and the back of the skull is relatively wider, suggesting relatively stronger neck muscles in *Tapirus* than in *Heptodon* (see p. 81). However, stronger cervical musculature might also be correlated with increased stresses resulting from the use of the proboscis. Another factor which may be pertinent here is orientation of the head. In *Heptodon* the occlusal plane diverges anteroventrally from the basicranial axis, while in *Tapirus* the occlusal plane is parallel or slightly anterodorsally inclined to the basicranium. This suggests that the head is held slightly more horizontally in *Tapirus* than it was in *Heptodon*, possibly in response to its relatively

heavier weight, or possibly because of the proboscis.

A second major factor which has been responsible for differences between the skulls of *Heptodon* and *Tapirus* is brain evolution. Evolution of the tapiroid brain will be described in a future paper. For the present discussion it will be sufficient to note that in tapiroids, as in equoids, a major feature of brain evolution (described in a classic work by Edinger, 1948) has been the expansion of the cerebral hemispheres and relative decrease in size of the olfactory bulbs. In *Heptodon*, the olfactory bulbs are relatively long, underlying most of the length of the frontals, and lie at the same level dorsally as the cerebrum. In *Tapirus*, the olfactory bulbs are relatively short, lying under only about the posterior third of the frontals, and the dorsal surface of the olfactory bulb chambers is at a lower level than that of the expanded cerebrum. The anterior part of the frontals is underlain by the posteroventrally-sloping nasal chamber. Since the ventral surface of the frontals immediately overlies the olfactory bulbs, and the dorsal surface must remain high to keep the nasal incision open, the external and internal tabulae of the frontal bone in *Tapirus* have become separated by a space, the frontal sinus. Thus, formation of the frontal sinus in *Tapirus* may be thought of as a response to the necessity of maintaining the nasals high above the orbits (to provide room for the proboscis beneath) when growth of the olfactory bulbs failed to keep pace with cerebral expansion and growth of the rest of the skull. (For a more thorough discussion of frontal sinus formation, see Edinger, 1950.)

As a direct result of cerebral expansion, the braincase of *Tapirus* is relatively wider than that of *Heptodon*. Sagittal and lambdoidal crests are relatively lower and do not project back as far in *Tapirus* as in *Heptodon*, perhaps because the expanded braincase provides more room for attachment of the temporal muscles in the modern form.

Or, on the other hand, the lower crests may reflect a relatively smaller amount of temporal musculature in *Tapirus*. The prominent sagittal and lambdoidal crests on the skull of *Heptodon* create a dorsal profile which diverges posterodorsally from the basicranial axis and occlusal plane. In *Tapirus pinchaque* the weaker crests and expanded frontal sinus result in a dorsal skull profile which parallels the basicranial axis.

The foramen ovale and postglenoid foramen have shifted posteriorly in *Tapirus* and are confluent with the foramen lacerum medium. Edinger and Kitts (1954) have pointed out that similar shifts in the position of the foramen ovale have occurred in equoids and rhinocerotoids. These changes may be related to the cerebral expansion that occurred in all three groups, but the exact reasons are still obscure.

The third major area in which changes have occurred during evolution of the skull from *Heptodon* to *Tapirus* involves the masticatory apparatus. The molar cusp pattern of *Tapirus* is similar to that of *Heptodon*, differing only in the following features: metacone more labially located, providing a slightly longer metaloph; ectoloph shorter (posterior to metacone apex) and relatively less prominent; paralophid and metalophid virtually nonexistent; M_3 hypoconulid absent. In *Heptodon*, molar shear occurs between the lingual side of the ectoloph and labial side of the paralophid and metalophid, as well as between upper and lower cross-lophs. As a result of the differences noted above, molar shear in *Tapirus* is almost entirely confined to the cross-lophs, with the anterior sides of protoloph and metaloph above shearing against the posterior sides of protolophid and hypolophid below. The functional advantage or adaptive significance of eliminating ectoloph shear and emphasizing cross-loph shear is not immediately apparent. This trend occurred in other tapiroid families besides the Tapiridae (Helaletidae and Deperetellidae) while in still other tapiroid families (Lophi-odontidae and Lophialetidae) ectoloph shear was retained, or even emphasized.

Probably the most important change from the dentition of *Heptodon* to that of *Tapirus* has been the molarization of the premolars. In *Heptodon* none of the premolars are molariform; in *Tapirus*, P^1 and P_2 are submolariform and the remaining premolars are molariform. As a result, the cheek tooth row is relatively longer and there is a relatively larger surface area available for mastication in *Tapirus* than in *Heptodon*. Perhaps in response to this increase in occlusal area at the front of the tooth row, the anterior border of the origin of the masseter (marked by a scar on the maxilla and malar below the orbit) has shifted forward relative to the tooth row, and is located above the anterior border of M^1 in *Tapirus*, compared with about the middle of M^2 in *Heptodon*. This increases the mechanical advantage of the masseter by lengthening its lever arm (distance from the masseter to jaw articulation) relative to the lever arm of the resistance (distance from teeth to articulation). The orbit also is located relatively more anteriorly in *Tapirus* than in *Heptodon*, and the anterior edge of the masseter scar is in the same position relative to orbit in both forms. Since the anterior part of the masseter takes origin from the bones forming the lateroventral border of the orbit, it is possible that the selective advantages resulting from a forward shift of the masseter were a significant factor in bringing about the change in position of the orbit. However, it should be kept in mind that in horses and other mammals the anterior origin of the masseter has moved forward independent of the orbit, by shifting onto the maxilla anterior to the orbit, and also that there are other functional advantages (related to proboscis development) involved in an anterior shift of the orbit.

Another change in dentition between *Heptodon* and *Tapirus* has been the atrophy of the upper canine and enlargement and caninization of the upper third incisor.

Thus, in *Tapirus*, the upper third incisor has replaced the canine functionally, and the upper tusk occludes in front of the lower, the reverse of the usual mammalian condition. This may be related to proboscis development if, with the proboscis extending in front of the premaxilla, the upper canine is located too far back to be effective. Another consideration is that the atrophy of the upper canine increases the amount of space available in the diastema for manipulation of food. Even without this additional space, the postcanine diastema is relatively longer in *Tapirus* than in *Heptodon*.

Finally, there are several features, in which the skull of *Tapirus* differs from that of *Heptodon*, which do not seem to be correlated with the three major developments discussed above. The optic foramen is smaller relative to the size of the skull and the other orbital foramina in *Tapirus* than in *Heptodon*. The tympanic, a simple half-ring in *Heptodon*, is expanded anteroventrally and laterally and forms a short floor to the external auditory meatus in *Tapirus*, although it is never large enough to form an inflated auditory bulla. The petrosal of *Tapirus* differs from that of *Heptodon* in having a shallower subarcuate fossa, a tegmen tympani composed of cancellous rather than solid bone, and in having a tympanohyal fused to it.

The mandible of *Tapirus* is fairly similar to that of *Heptodon*, differing from the latter in having a more procumbent symphysis (in correlation with the downcurved premaxillae), a posteriorly curved coronoid process (which may increase the mechanical efficiency of the temporalis), a slightly more rounded angle, and a relatively shorter and wider condyle.

SKULL EVOLUTION

The few known skulls of fossil tapiroids reveal some of the intermediate stages in the evolutionary developments discussed above and provide information on the rates at which the changes took place.

In a late early Eocene specimen of *Heptodon calciculus* (AMNH 294), the nasal incision extends back to a point over P^1, and the premaxillae no longer contact the nasals. In the middle Eocene genus *Helaletes*, which may have included species near the ancestry of the Tapiridae, the nasal incision is tremendously enlarged, both dorsoventrally and posteriorly, and extends back as far as P^3. The anterior wall of the orbit is over M^1, and there is a groove for the nasal diverticulum on the ascending process of the maxilla. However, the nasals of *Helaletes* are unshortened and extend as far forward as the anterior border of the premaxillae. This suggests that *Helaletes* did not have a prehensile proboscis, since the long nasals would have restricted its mobility.

The next stage in cranial evolution in the line leading to modern tapirs is represented by the latest Eocene or early Oligocene species *Colodon? hancocki* (known from a few specimens in collections of the University of Oregon Museum of Natural History). In *Colodon? hancocki* the nasal incision is extended slightly more posteriorly than in *Helaletes*, but is not quite as deep posteroventrally. However, the nasals are shorter in *C.? hancocki*, extending only to to a point over the postcanine diastema. This suggests that by the beginning of the Oligocene ancestral tapirids had a proboscis which, judging from the degree of retraction of the nasal incision and nasal shortening, may have been almost as long as that of modern tapirs.

A North American late Oligocene skull of *Protapirus* (PU 10899), the most primitive known tapirid, was described and figured by Hatcher (1896). Scott (1941, p. 754 and pl. 79) provided a few additional observations and new illustrations, with the premaxillae, which are missing in the Princeton skull, restored from a second skull (South Dakota School of Mines 2829). Modifications for the proboscis in the late Oligocene *Protapirus* skull are in about the same stage of development as in *Colodon?*
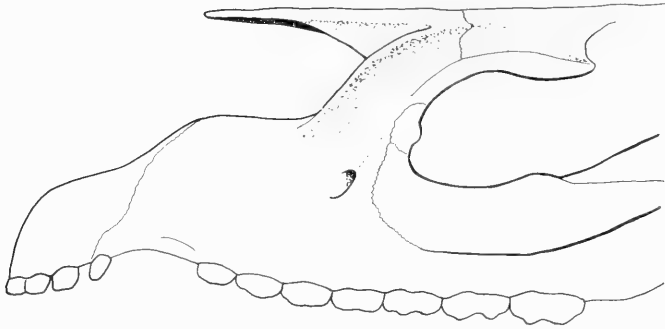
Fig. 4. *Protapirus.* Restoration of anterior half of skull, based mainly on PU 10899. Compare with Fig. 1. × ½.

hancocki. The nasal incision extends back to a point over P^4, and the anterior edge of the orbit is over the middle of M^1. The nasals terminate slightly anterior to P^1. A broad groove for the nasal diverticulum extends up the ascending process of the maxilla, arches posteriorly into the dorsal surface of the prominent supraorbital process of the frontal, and continues back to the posterior border of the supraorbital process. This is a marked difference from the condition in *Tapirus,* where the supraorbital processes are suppressed and the groove for the nasal diverticulum curls medially and anteriorly to terminate on the posterior border of the nasals.

Both Hatcher's and Scott's illustrations of the Princeton *Protapirus* skull (drawn from the left side) show a deep groove on the anterior portion of the maxilla, parallel to the groove for the nasal diverticulum and separated from it by a high ridge. Examination of the right side of the skull shows that this anterior groove is an artifact, due to a break and inward crushing of the anterior part of the left maxilla. A new restoration of the anterior half of the skull of *Protapirus* is shown in Figure 4.

The nasal incision is narrower in *Protapirus* than in *Tapirus* because the anterior part of the maxilla is higher (less excavated) and the nasals are lower in the Oligocene genus. Scott (*loc. cit.*) considered the differences between the two forms great enough to suggest that in *Protapirus* the proboscis was only in an incipient stage. However, in Scott's restoration the nasal incision is drawn too narrow. In my opinion the nasal incision is large enough and the nasals are short enough in *Protapirus* to suggest that it had a fairly versatile proboscis.

There is still a marked postorbital constriction and the supraorbital processes are prominent in *Protapirus,* indicating that the nasal chamber did not extend back between the orbits in that genus. The premaxillae arch downwards, as in *Tapirus,* although the upper third incisor is not enlarged. The upper canine, however, is about as small as in the modern tapir. This indicates that the third incisor was enlarged after the atrophy of the canine, probably to functionally replace the upper canine in shear against the lower canine. The premolars are still non-molariform to submolariform in *Protapirus.* The foramen ovale and postglenoid foramen are confluent with the foramen lacerum medium in *Protapirus.*

Although *Protapirus* possesses all the features one would expect to find in the ancestor of *Tapirus,* the known species of *Protapirus* appear too late in time to be directly ancestral to modern tapirs. Schuab (1928) described under the name *Tapirus helvetius* the anterior half of an almost modern tapirid skull from Europe, which he considered on the basis of lithological correlation to be of middle or late Oligocene age. Cranial

modifications for the proboscis are more ad-vanced in *Tapirus helvetius* than in *Protapirus* in the following features: the nasal incision extends more posteriorly, reaching to a point over the orbit; the anterior part of the maxilla is lower and the nasals appear to be located slightly higher, leaving a deeper nasal incision; The groove for the nasal diverticulum curls onto the posterior border of the nasals, as in modern tapirs; the supraorbital processes are less pronounced. The anterior part of the skull of *Tapirus helvetius* is basically like that of *Tapirus pinchaque*, differing only in the following features: the nasal incision is not quite as deep posteroventrally, partly because a long posterior process of the premaxilla extends back over the maxilla to a point above the posterior edge of P^4; the nasals appear to be located slightly lower in the Oligocene species. Thus on the basis of anterior cranial morphology, *Tapirus helvetius* is intermediate between *Protapirus* and modern tapirs, but definitely closer to the latter. The same is true for its dentition— the premolars of *T. helvetius* are almost, but not quite, molariform.

Another tapirid close in age and similar in morphology to *Tapirus helvetius* was described by Schlaikjer (1937) under the name *Miotapirus harrisonensis*. This form, known only from the anterior half of a skull and a few limb bones (MCZ 2949) from early Miocene deposits in Wyoming, displays proboscis modification about as in *Tapirus helvetius*, except that the posterior process of the premaxilla is shorter, extending back to a point above P^2, and the nasals appear to be slightly higher. The skulls of *Tapirus helvetius* and *Miotapirus harrisonensis* indicate that by about the end of the Oligocene, or over 25 million years ago, cranial modifications for the tapirid proboscis were in essentially the same stage as in the recent species *Tapirus pinchaque*.

One of the major steps in the evolution of the proboscis was the tremendous enlargement of the nasal incision that occurred during the relatively short period of time between early Eocene *Heptodon* and middle Eocene *Helaletes*. Since the nasals were unshortened in *Helaletes* it seems unlikely that it had a proboscis; this suggests that the reasons for the initial enlargement of the nasal incision were probably not related to proboscis development. Primitively in perissodactyls the nasal diverticulum is lodged in the nasal incision. Enlarged nasal diverticula apparently have created depressions in the maxillary walls (preorbital fossae) and caused enlarged nasal incisions in many extinct perissodactyls (see Gregory, 1920). It therefore seems possible that expansion of the nasal diverticulum may have been responsible for the enlargement of the nasal incision in *Helaletes*. With the nasal incision enlarged, tapiroids would then have been preadapted for proboscis development.

Hyoid arch: Fragments of the hyoid arch are preserved in MCZ 17670, but most of the elements are too incomplete to yield much information. Neither ceratohyals nor thyrohyals were fused to the basihyal in *Heptodon*, and there is a long, low, irregular lingual process on the basihyal. In *Tapirus*, the thyrohyals are fused to the basihyal, and there is no lingual process.

AXIAL SKELETON

Vertebrae (Fig. 5): The vertebrae known for *Heptodon* include all the cervicals (except the fifth), the first two thoracic, and the last lumbar. In the atlas, the vertebrarterial canal enters at the posterior edge of the transverse process and emerges a short distance anteriorly on the ventral side. The atlantal (or alar) groove is open, notching the anterior edge of the transverse process. The neural spine of the last lumbar vertebra is only very slightly cranially inclined, which suggests reduced mobility of the vertebral column (Slijper, 1946, p. 103).

Vertebrae of *Tapirus* differ from those of *Heptodon* in the following features: cervical vertebrae relatively shorter and wider, with
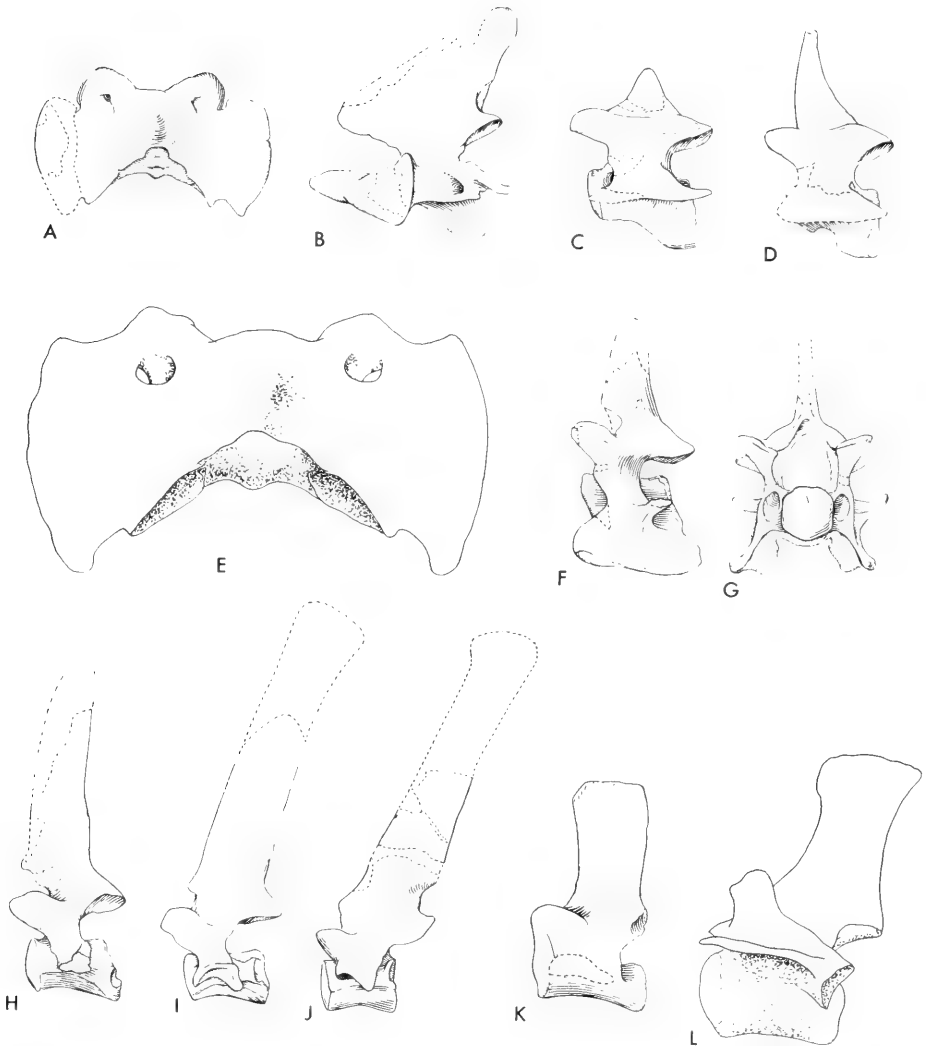
Fig. 5. Vertebrae of *Heptodon posticus* (MCZ 17670) and *Tapirus pinchaque* (AMNH:M 149424). A, E, dorsal views of atlases of *H. posticus* and *T. pinchaque*, respectively. B, C, D, lateral views of axis and third and fourth cervical vertebrae of *H. posticus*. F, G, lateral and anterior views of sixth cervical vertebra of *H. posticus*. H, I, J, lateral views of seventh cervical and first and second thoracic vertebrae of *H. posticus*. K, L, lateral views of last lumbar vertebra of *H. posticus* and *T. pinchaque*, respectively. All × ½.

anterior ends of centra more convex and posterior ends more deeply concave; atlantal groove of atlas bridged over by anterior growth of transverse process; odontoid process of axis relatively shorter and broader; neural spine of fourth cervical vertebra lower; postzygapophyses of first thoracic vertebra facing more laterally (and less

ventrally); neural spine of last lumbar vertebra slightly caudally inclined.

The shorter, wider and more opisthocoelous cervical vertebrae of *Tapirus* indicate a more powerful neck in the modern tapir than in *Heptodon*, probably in response to the needs of supporting a relatively larger and heavier head. The atlantal groove of

the atlas is bridged over in all modern perissodactyls and may simply reflect expansion of transverse processes to provide greater area for muscle attachment. The more laterally-facing postzygapophyses of the first thoracic vertebra restrict lateral movement but strengthen articulation between it and the following vertebra. The trend from cranial to caudal inclination of lumbar neural spines is correlated with decreasing importance of the longissimus muscles as spinal flexors and a backwards shift in their insertion from lumbar to sacral vertebrae. This results in decreased mobility of the vertebral column and is often correlated with increasing body weight (Slijper, 1946, pp. 103–104).

APPENDICULAR SKELETON

Scapula (Fig. 6): Only the glenoid end of the scapula is known for *Heptodon* but a fairly accurate restoration of the entire bone may be made by extrapolating from complete scapulae known for the early Eocene equoid *Hyracotherium* (figured in Kitts, 1956, pl. 2, fig. 1) and the middle Eocene tapiroid *Helaletes* (several specimens in collections of the United States National Museum). The posterior border is straight, the vertebral border straight to gently convex, and the anterior border more strongly convex. The neck is moderately constricted. The spine extends ventrally almost to the glenoid and is high at its ventral border. It has a small tuber spinae and a relatively prominent acromion. Infraspinatus and supraspinatus fossae are about equal in area. The tuber scapulae is low and bears a small coracoid process.

In *Tapirus* the spine is reduced ventrally, terminating more dorsally than in *Heptodon*, and bears no acromion. The ventral reduction of the spine accentuates the prominence of the tuber spinae. There is no projecting coracoid process and the tuber scapulae is considerably higher and more prominent, and forms the ventral border

Fig. 6. Right scapula. Left, *Heptodon posticus*, hypothetical restoration, × ½. Right, *Tapirus pinchaque*, MCZ:M 6037, × ⅓.
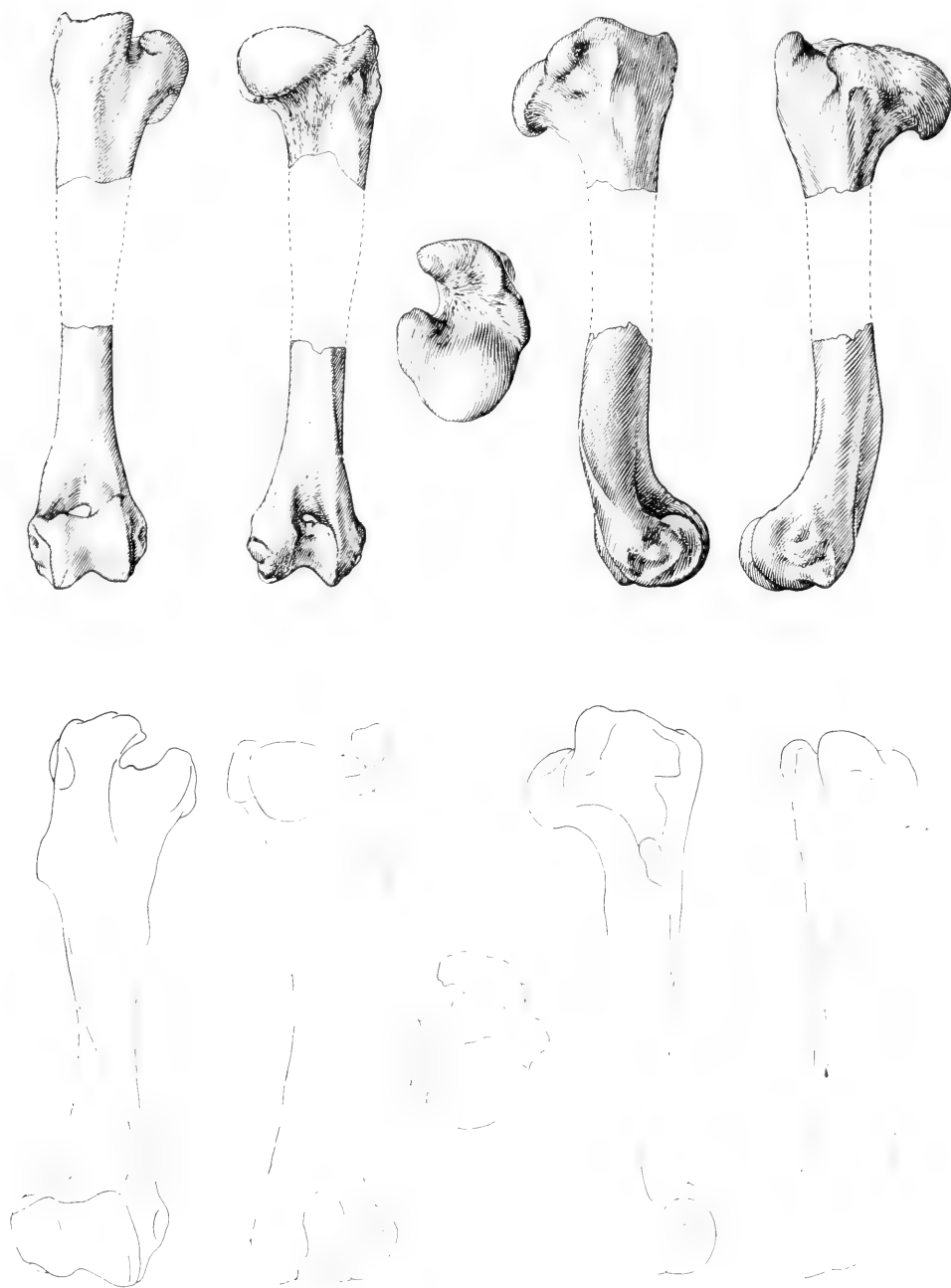
Fig. 7. Right humerus. Above, *Heptodon posticus*, MCZ 17670, in, from left to right, anterior, posterior, proximal, lateral and medial views. × ½. Below, *Tapirus pinchaque*, MCZ:M 6037, same views. × ¼.

of a deep coracoscapular (or supraspinous) notch.

Reduction of the acromion is an advanced feature in perissodactyls and appears to be correlated with loss of the clavicle. *Heptodon* may have still had a clavicle but if so, it probably was relatively small and did not articulate with the scapula. The absence of an acromion in *Tapirus* is reflected in modifications of the muscles which originally attached to that part of the scapula. These include the levator scapulae ventralis, which typically originates on the transverse processes of the atlas and inserts on the acromion, and the acromiodeltoid, which originates on the acromion and inserts on the deltoid tuberosity of the humerus. According to Campbell (1936, p. 206), in *Tapirus terrestris* the levator scapulae ventralis and acromiodeltoid have fused to form the transversohumeralis, which originates on the wing of the atlas and inserts on the fascia of the lateral head of the triceps.

A deep coracoscapular notch distinguishes scapulae of *Tapirus* from those of all other perissodactyls. The notch is formed by the dorsal expansion of the prominent tuber scapulae, possibly to extend the area available for attachment of the biceps. This expansion restricts the space open in front of the narrow neck of the scapula, thus forming the notch. The suprascapular artery and nerve pass through the coracoscapular notch. In life the notch is closed by a tendinous band which extends from the tip of the tuber scapulae to the anteroventral edge of the anterior border of the scapula.

Humerus (Fig. 7): The humerus of *Heptodon* is relatively long and slender. In MCZ 17670 it is 34 mm wide across the distal epicondyles and, judging from the proportions of the parts preserved, probably was about 150 mm long. The lateral (greater) tuberosity is raised slightly above the level of the head and extends anteriorly and then curves medially. The medial (lesser) tuberosity is short and low, and not distinctly separated from the head. The bicipital groove is undivided and relatively deep and narrow. Much of the proximal half of the shaft is missing in MCZ 17670 and the proximal quarter is gone in AMNH 294 (*Heptodon calciculus*), but between the two specimens enough is preserved to indicate that the deltoid crest and tubercle were not prominent. The teres tubercle is not evident in AMNH 294; either the teres major left no attachment scar or it inserted relatively far proximally (on the missing proximal quarter of the shaft).

The supinator crest is relatively low but sharp-edged, and flares out posterolaterally along the distal third of the shaft. The coronoid (supratrochlear) fossa is relatively broad and shallow, and the olecranon (anconeal) fossa slightly narrower and deeper. The thin wall of bone separating the two is perforated but this may be artificial. The trochlea is asymmetrical, narrowing laterally. At the proximal end of the trochlea there is a thin strip of lateral condyle which rapidly narrows and terminates distally. Lateral and medial epicondyles are about equally prominent and both are relatively low.

The humerus of *Tapirus* differs from that of *Heptodon* in the following features: lateral tuberosity higher, with a more prominent, medially-directed anterior hook which is separated from the main ridge by a broad groove; medial tuberosity higher, raised above the level of the head and almost as high as the lateral tuberosity, separated from the head by a low groove, and with its medial face vertical; bicipital notch relatively wider; deltoid tubercle prominent, located almost one-third of the way down the shaft, with a narrow ridge continuing distally from it almost to the coronoid fossa; teres tubercle prominent, located one-third to one-half of the way down the shaft; supinator ridge not as extended proximally and blunter at its proximal end; distal end of shaft deeper anteroposteriorly; lateral condyle wider; coronoid fossa shallower, olec-
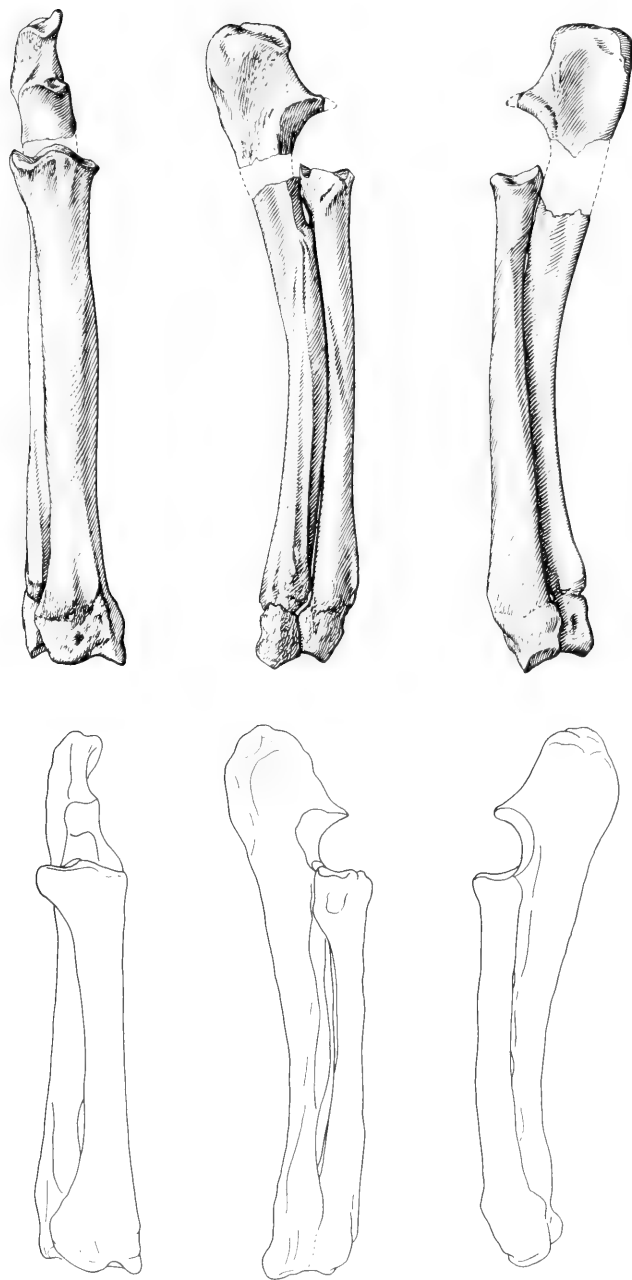
Fig. 8. Right radius and ulna. Above, *Heptodon posticus*, MCZ 17670, in, from left to right, anterior, lateral, and medial views. $\times \frac{1}{2}$. Below, *Tapirus pinchaque*, MCZ:M 6037, in same views. $\times \frac{1}{4}$.

ranon fossa deeper, separated by very thin but unperforated sheet of bone; lateral epicondyle more massive and more posteriorly extended.

The more prominent tuberosities and tubercles for muscle attachment, the distal displacement of deltoid and teres tubercles, and the larger lateral epicondyle on the humerus of *Tapirus* correlate with the increased size and relatively heavier body of the modern tapir compared with that of *Heptodon*. Such modifications appear in all lines of perissodactyls with increase in size. The wider lateral condyle hinders lateral motion and thus stabilizes anterior–posterior movement at the elbow joint.

Radius (Fig. 8):   The radius of *Heptodon posticus* in MCZ 17670 measures 139 mm long and 25 mm wide across the proximal end. The shaft is anteroposteriorly compressed and slightly arched anteriorly. The humeral facet is relatively short (anteroposteriorly) and wide, and divided into two shallow concavities, the lateral one shorter and wider than the medial one. A slightly roughened area on the anterior face of the shaft a short distance below the humeral facet marks the lateral end of the insertion of the biceps; the biceps aponeurosis probably extended around onto the medial side of the radius. A vertical scar on the anteromedial edge and medial side of the shaft, beginning about 20 mm below the proximal end, indicates the insertion of the brachialis and possibly also a medial collateral ligament. Just below the humeral facet on the lateral side of the shaft a small tuberosity marks one part of the origin of the lateral digital extensor (extensor digiti quinti proprius), and probably the insertion of lateral collateral ligaments. A line which begins about one-quarter of the way down the lateral side of the shaft and curves anteriorly as it descends, marks the anterior edge of the radial origin of the extensor carpi obliquus (abductor pollicis longus).

On the posterior side of the shaft, just below the humeral facet, there is a narrow facet for articulation with the ulna. Below this facet there begins a roughened and slightly excavated area marking the attachment of the interosseus ligaments which bound the radius to the ulna. Proximally, this scar extends across the entire width of the shaft, but about halfway down it is confined to the lateral side of the shaft. About 15 mm below the proximal end of the shaft the scar is interrupted by the interosseus space, a smooth area marked by the passage of the interosseus artery.

The distal end of the shaft of the radius is somewhat expanded and bears on its anterior face a broad groove for the passage of the tendon of the extensor carpi radialis. A small facet for articulation with the distal end of the ulna is present on the posterolateral corner. The distal end of the radius bears a large, anterolaterally concave, posteriorly convex facet for the scaphoid and an anteriorly concave, posteriorly convex facet for the lunar.

Ulna (Fig. 8):   The ulna has a mediolaterally compressed, anteriorly arched shaft, and a moderately large olecranon process. The anterior edge of the shaft is roughened along its entire length, except for small proximal and distal facets for the radius and a small interosseus space, indicating that the ulna was firmly and probably immovably bound by interosseus ligaments to the radius. The olecranon is slightly concave medially and expanded on proximal and posterior sides. A large rounded prominence occupying the posterior half of the end of the olecranon marks the main area of insertion of the long head of the triceps; the lateral and medial heads of the triceps inserted on lateral and medial sides, respectively, below the insertion of the long head.

The lateral side of the shaft of the ulna bears a long vertical scar from the origin of part of the lateral digital extensor and, between this and the radius, is roughened from the attachment of the oblique carpal
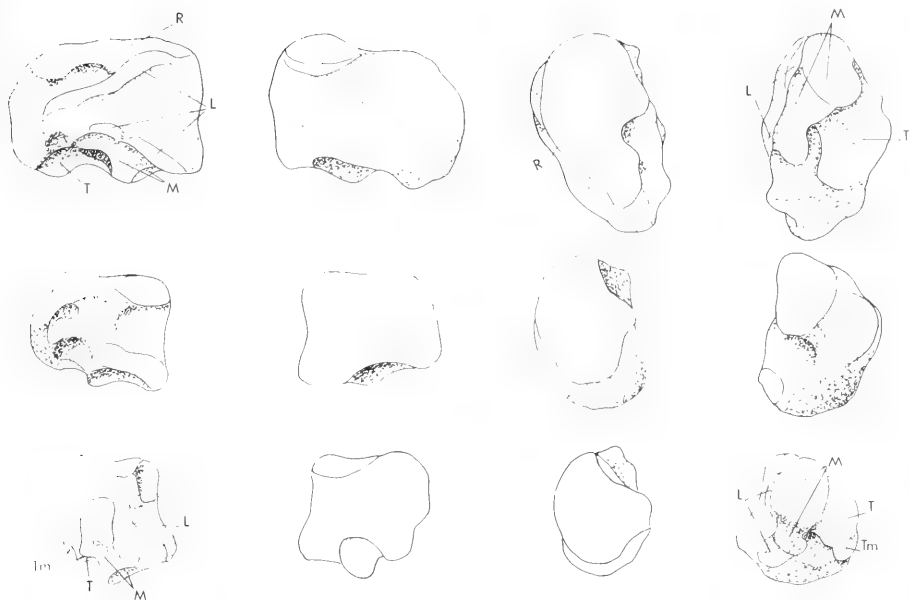
Fig. 9. Right scaphoid. Top row: *Heptodon posticus*, MCZ 17670, in, from left to right, lateral, medial, proximal and distal views. × 1½. Middle row: *Protapirus obliquidens*, AMNH 662 (reversed), × ¾. Bottom row: *Tapirus pinchaque*, YPM 204, × ½. Letters indicate articular contacts. For abbreviations see p. 102.

extensor. The anterior edge of the medial side of the ulna bears scars just below the coronoid crest, marking the insertions of the biceps and brachialis. Distally, the shaft of the ulna is excavated to fit the swollen distal end of the radius, and there is a small anteromedial facet for articulation with the radius. The distal end of the ulna bears a roughly square, saddle-shaped facet for articulation with the cuneiform and, posterior to it, a slightly smaller, triangular, convex, posteromedially-facing facet for the pisiform.

The radius and ulna of *Tapirus* differ from those of *Heptodon* in the following features: radius and ulna fused together proximally and distally; humeral facet of radius further extended laterally, and lateral tuberosity more prominent; distal end of radius wider, with most of the expansion on the lateral side; facet for lunar (at distal end of radius) shorter anteroposteriorly.

Carpus: The carpus, seen in anterior view, is relatively low and wide, with the lunar resting mainly on the unciform. The scaphoid (see Fig. 9) is relatively long (anteroposteriorly) and low, with a large posterior process. The proximal surface is covered by an anteromedially convex, posterolaterally concave facet for the radius, and the lateral side bears narrow proximal and distal strips for articulation with the lunar. On the distal surface there are two lateral facets, the posterior one steeply inclined and the anterior one horizontal, for the magnum, and a large medial facet for the trapezoid. There is no evidence of a facet for the trapezium.

The lunar (see Fig. 10) is relatively high and narrow in anterior view. The facet for the radius is wide and anteroposteriorly convex anteriorly, and narrow and relatively flat posteriorly. The medial side has narrow proximal and central facets for the scaphoid and, anteriorly, a large, vertical, distal facet for the magnum. Posteriorly, the mediodistal edge is truncated by a large concave facet for the hump of the magnum.
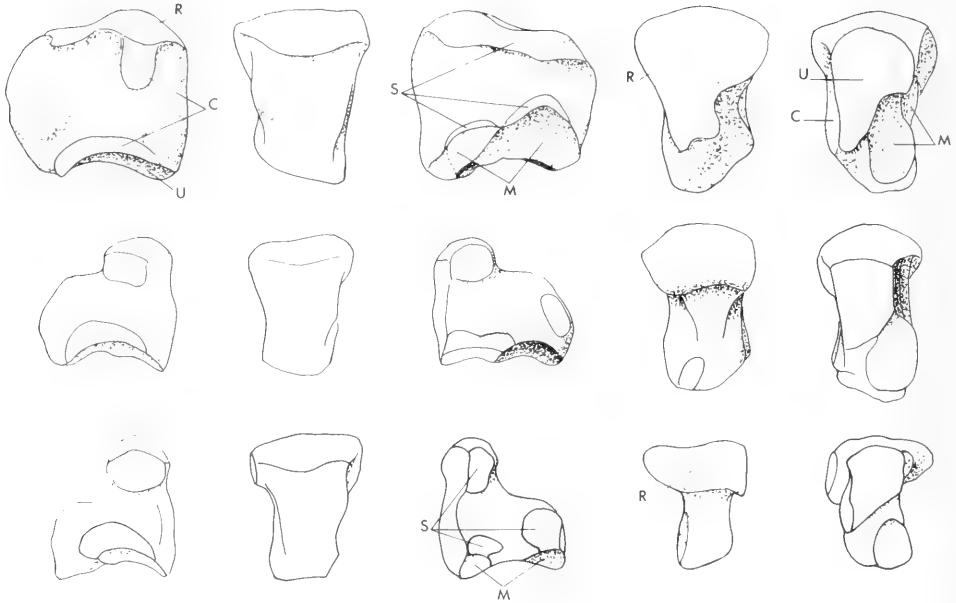
Fig. 10. Right lunar. Top row: *Heptodon posticus,* MCZ 17670, in, from left to right, lateral, anterior, medial, proximal, and distal views. × 1½. Middle Row: *Protapirus obliquidens,* AMNH 662 (reversed), × ¾. Bottom row: *Tapirus pinchaque,* YPM 204, × ½. Letters indicate articular contacts.

Anteriorly, the distal surface is covered by an anteroposteriorly concave, horizontal facet for the unciform. The lateral side has relatively small proximal and distal facets for the cuneiform.

The cuneiform (see Fig. 11) has a roughly square, anteroposteriorly concave, slightly lateromedially convex ulnar facet, and a slightly smaller, elongate, posteriorly inclined pisiform facet. The medial side has relatively short proximal and distal facets for the lunar, and the distal surface bears a large, triangular, concave facet for the unciform.

The pisiform (see Fig. 11) has approximately equal-sized facets for ulna and cuneiform, and a relatively flat, slightly proximodistally expanded posterior process. A prominent tubercle on the anterior end of the medial side may have served for the attachment of ligaments which bound the pisiform to the rest of the carpus.

The trapezium (see Fig. 12) is a small, relatively flat, disc-shaped bone, with a large lateral facet for articulation with the trapezoid. The trapezoid is relatively long anteroposteriorly and low, with a large, saddle-shaped facet for the scaphoid occupying the proximal surface, and a facet for the second metacarpal covering most of the distal surface. Facets for the magnum and trapezium occur on lateral and posteromedial sides, respectively.

The magnum (see Fig. 12) has an approximately square anterior face, a short, high dorsal hump, and a large posterior process. Articulation with the scaphoid is in two parts, a horizontal anterior facet and an almost vertical posterior one (on the medial side of the dorsal hump). Articular facets for the lunar, on the other hand, are vertical in front and more horizontal (laterodistally inclined) behind, with the posterior one covering the top of the dorsal hump. On the medial side there are facets for the trapezoid and second metacarpal, and on the lateral side, below the anterior lunar facet, a small facet for the unciform.
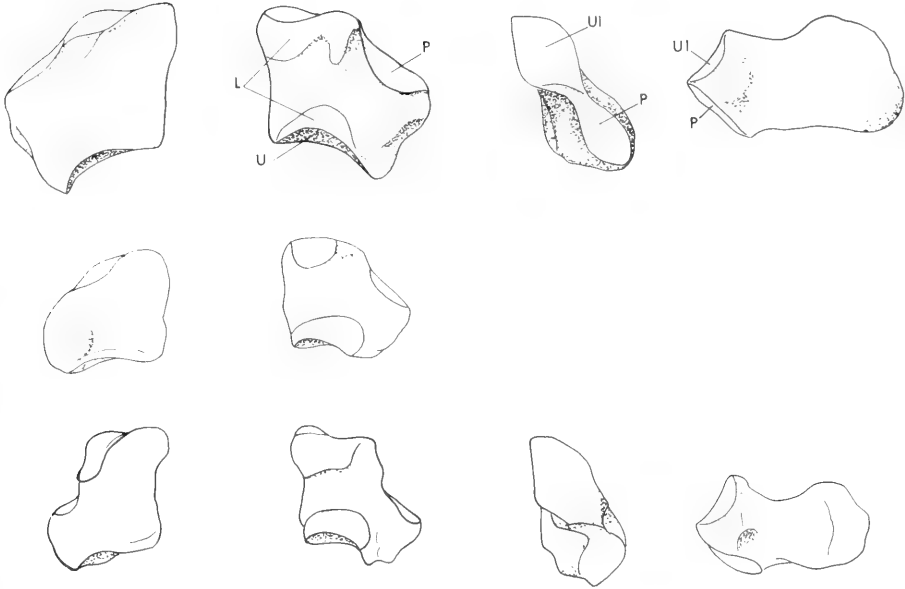
Fig. 11. Right cuneiform and pisiform. Top row: *Heptodon posticus*, MCZ 17670, cuneiform in lateral, medial and proximal views, and pisiform in medial view. × 1½. Middle row: *Protapirus obliquidens*, AMNH 662 (reversed) × ¾. Bottom row: *Tapirus pinchaque*, YPM 204, × ½. Letters indicate articular contacts.

A saddle-shaped facet for the third metacarpal occupies the anterior half of the distal surface.

The unciform (see Fig. 12) is about as high as it is wide, and has a relatively short, stubby posterior process. The proximal surface bears approximately equal-sized, slightly convex lunar and cuneiform facets. Along the curving mediodistal edge there is a small proximal facet for the magnum, a central facet for the proximolateral edge of the third metacarpal, and a large, posteriorly-expanded distal facet for the fourth metacarpal. The same articular strip continues proximolaterally for articulation with the fifth metacarpal.

Metacarpals: There is no evidence of a first metacarpal. The second metacarpal is 72 mm long and 11 mm wide at the distal end. It has a relatively long, saddle-shaped facet for the trapezoid, a narrow lateral articular strip for the magnum, and a postero-medial facet for the trapezium. A broad, low tuberosity on the posterior side, im-

mediately below the trapezoidal facet, may have served for attachment of the flexor carpi radialis, or possibly a carpal ligament.

The third metacarpal is 83 mm long and 14 mm wide across the distal condyle. At the proximal end there is a large, antero-posteriorly convex, mediolaterally concave, facet for the magnum, and a smaller antero-laterally-facing facet for the unciform. A low prominence on the medial side of the anterior face, just below the magnum facet, marks the insertion of the extensor carpi radialis. The shaft of the third metacarpal is triangular in cross section proximally and flat distally, with posterolateral and postero-medial sides roughened proximally for the attachment of the interossei. The distal condyle is evenly convex and has a prominent medial keel on the posterior half. Two pits on the posterior face, immediately above the condyle, accommodated the proximal ends of the sesamoids. On each side of the condyle a deep pit surmounted by a low tuberosity marks the attachment of deep

Fig. 12. Right distal carpals. In each pair of rows *Heptodon posticus*, MCZ 17670, is above, $\times 1\frac{1}{2}$, and *Tapirus pinchaque*, YPM 204, is below, $\times \frac{1}{2}$. Top two rows: From left to right, trapezium in medial and lateral views, and trapezoid in lateral, anterior, medial, proximal and distal views. Middle two rows: magnum in lateral, medial, proximal and distal views. Bottom two rows: unciform in lateral, anterior, medial, proximal and distal views.   Letters indicate articular contacts.

and superficial layers, respectively, of collateral ligaments. The distal ends of the second, fourth, and fifth metacarpals are similar to that of the third, but are transversely compressed and asymmetrical.

The fourth metacarpal has approximately the same dimensions as the second. It has a large triangular proximal facet for the unciform and a small lateral facet for the fifth metacarpal. The fifth metacarpal is 58 mm long and 9 mm wide distally, with an elongate, saddle-shaped unciform facet and a narrow medial facet for the fourth metacarpal.

Phalanges: The proximal phalanx of the medial digit is about 21 mm long. Prominent raised areas on the posterior face just below the metacarpal facet served for attachment of the collateral ligaments; the sesamoidean ligaments probably inserted on the area between them. Tuberosities on left and right sides at the distal end of the posterior face probably mark insertions of parts of the tendo perforatus (superficial digital flexor tendon). On either side of the distal articular facet, a shallow pit surmounted by a low tuberosity indicates the attachment area of the collateral ligament and suspensory ligament of the navicular sesamoid.

The second phalanx of the third digit is about 13 mm long and 13 mm wide across its proximal end. Low prominences at the proximal end of the posterior face served for insertion of part of the tendo perforatus, and, laterally, the collateral ligaments. Shallow depressions on each side of the distal condyle indicate attachment areas of collateral ligaments to the third phalanx.

The third, or ungual, phalanx of the median digit measures about 20 mm long and has a maximum width of 16 mm. The medial fissure is very short. A large raised area on the proximal end of the posterior surface marks the insertion of the tendo perforans (deep digital flexor tendon). On either side of this raised area, shallow depressions indicate the insertion areas of the collateral
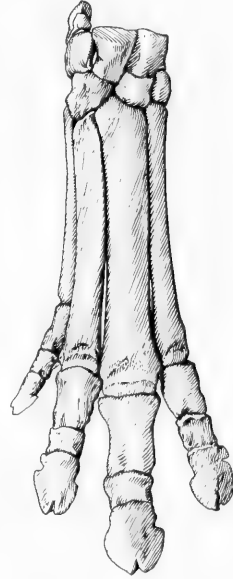
Fig. 13.   Right manus of *Heptodon posticus*.   MCZ 17670. × ½.

ligaments. Two large foramina above the tendo perforans prominence served for the entrance of the digital arteries into the ungual. Phalanges of the other digits are similar to those of the third, but are asymmetrical and more transversely compressed.

The complete manus of *Heptodon posticus* is shown in Figure 13.

The manus of *Tapirus* differs from that of *Heptodon* in the following features: Scaphoid shortened by truncation of the posterior tuberosity and posterior end of the radial facet; trapezium-scaphoid articulation present; scaphoid-lunar articular facets relatively higher (proximodistally), the proximal one confined to the anterior end and oriented posterolaterally so that the scaphoid curves behind the anterior edge of the lunar. Lunar with posterior part of proximal surface excavated so that the radial facet is confined to the anterior third of the bone and the proximal half of the posterior tuberosity is missing; distal lunar-cuneiform and lunar-unciform articulations shorter posteriorly; lunar-magnum facets

more horizontally oriented; posterior lunar-magnum facet relatively smaller. Cuneiform with posterior part of proximal surface lower, resulting in a more distally located pisiform facet. Trapezium relatively higher. Trapezoid relatively shorter (anteroposteriorly) and higher, with less of a posterior process. Magnum with a relatively lower and wider anterior face and a shorter and less pointed posterior process; magnum-unciform articulation relatively higher, but lacking a separate posterior facet; magnum-second metacarpal facet higher proximodistally. Metacarpals relatively shorter and wider.

The main difference between the front foot of *Tapirus* and that of *Heptodon* is in the radio-carpal joint. The truncation of the posterior end of the scaphoid and lowering of the posterior half of the lunar produces a posteriorly-shortened articulation between the radius and the scaphoid and lunar. This difference, plus the lower pisiform facet on the cuneiform, suggests greater freedom for flexion at this joint in *Tapirus*. The lateral extension of the proximal surface of the scaphoid behind the proximal facet of the lunar strengthens the scapho-lunar articulation and also provides additional support for the radius (possibly to compensate for the shortened radio-lunar articulation). Most of the other differences listed above are either related to the modification just discussed or, like the more horizontal lunar-magnum facets, result from the greater weight of *Tapirus*.

The manus of *Protapirus* was described and figured most recently by Scott (1941, pp. 756–758, pl. 80, fig. 2), based on a late Oligocene specimen (AMNH 662). It is generally quite similar to the manus of *Tapirus*, but slightly more primitive in the following features: scaphoid and trapezoid relatively longer anteroposteriorly; posterior process of lunar and cuneiform relatively
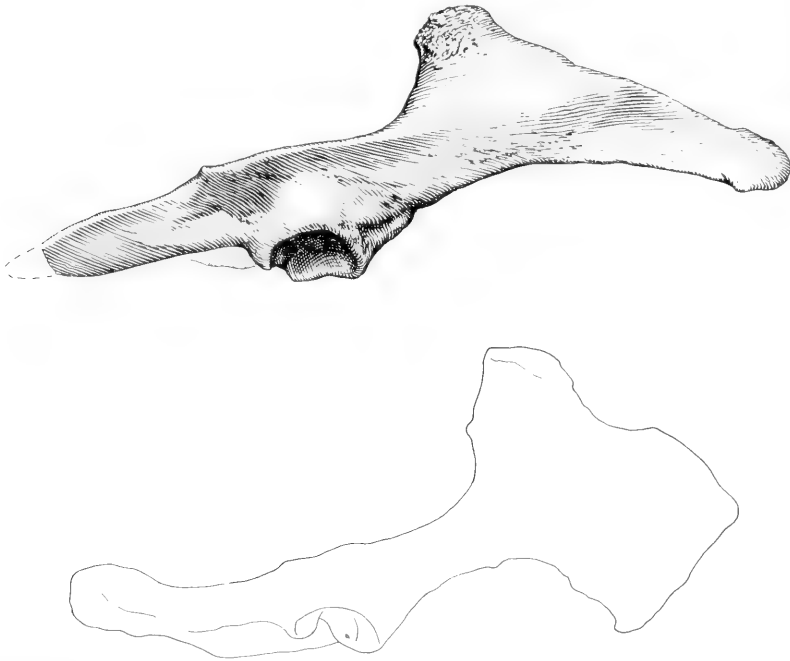
Fig. 14. Right innominate. Above, *Heptodon posticus*, MCZ 17670, lateral view, × ½. Below, *Tapirus pinchaque*, MCZ:M 6037. × ¼.

higher; distal lunar-cuneiform articulation extends further posteriorly; trapezium extends posterolaterally instead of posterodistally. The manus of *Protapirus* further differs from that of *Tapirus* in having a relatively larger trapezium, a more posteriorly and more proximally located scaphoid-lunar articulation, and relatively shorter phalanges. On the scaphoid the posterior lunar facet is separated from the trapezoid facet by a large fossa. The carpus of *Protapirus* is not relatively longer and narrower than that of *Tapirus*, contrary to the statements of Scott (*op. cit.*, p. 758).

A second manus of *Protapirus* (Univ. Calif. Mus. Paleo. 934), representing *P. robustus*, a larger species than the one Scott described, differs in no appreciable way from AMNH 662 except in larger size.

The lunar, cuneiform, and pisiform are all that is known of the carpus of the early Miocene genus *Miotapirus*. The posterior processes of the lunar and cuneiform are as low in *Miotapirus* as in *Tapirus*, but the distal lunar-cuneiform articulation is still longer and the posterior scaphoid facet of the lunar more posteriorly and proximally located than in the modern tapir.

Innominate (Fig. 14): The blade of the ilium is expanded dorsally into a relatively
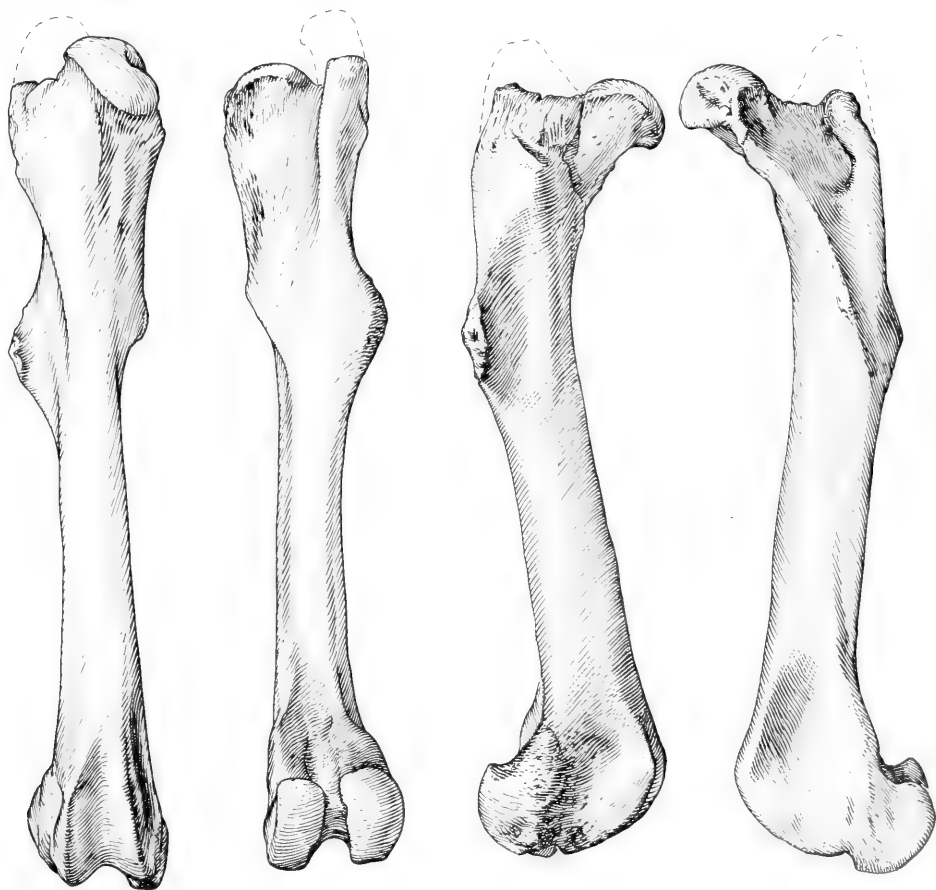
Fig. 15. *Heptodon posticus.* MCZ 17670. Right femur in, from left to right, anterior, posterior, lateral and medial views. × ½.

Fig. 16. *Tapirus pinchaque.* MCZ:M 6037. Right femur in, from left to right, anterior, posterior, lateral and medial views. ✕ ¼. Compare with Fig. 15.

narrow tuber sacrale, and extends relatively far anterolaterally to terminate in a narrow tuber coxae. Between these two tuberosities, the iliac crest is straight. The shaft of the ilium is relatively long and narrow. On the lateral side, just in front of the acetabulum, a prominent groove and ridge mark the origin of the lateral tendon of the rectus femoris. The ischiatic spine is located on the dorsal border a short distance posterior to the acetabulum. The posterior end of the ischium is broken off, but judging from its condition in *Hyrachyus* and *Helaletes*, it probably was considerably shorter than the ilium, and the tuber ischii was probably relatively weak. Pelvic girdles in which the ilium is relatively long and pubo-ischiac portion relatively short are characteristic of cursorial ungulates, and indicate an increase in importance of the gluteal muscles (which originate on the blade of the ilium) over those of the pubo-ischiac group in extension

of the femur (Smith and Savage, 1956, pp. 612–614).

The innominate of *Tapirus* differs from that of *Heptodon* in having a much wider, more vertically expanded, tuber coxae, and relatively larger sacral and ischial tuberosities. The tuber coxae serves for attachment of the external and internal obliquus abdominis muscles, the tuber sacrale for sacral ligaments medially and parts of the gluteus medius and longissimus dorsi on its lateral surface, while the tuber ischii serves for the origin of biceps femoris, semimembranosus, and semitendinosus. The greater prominence of these tuberosities in the modern tapir probably correlates with its larger size and relatively heavier body.

Femur (Fig. 15):   The femur of *Heptodon posticus* measures about 205 mm long from head to distal condyles) and 37 mm wide across the distal end. The top of the greater trochanter has been broken off in
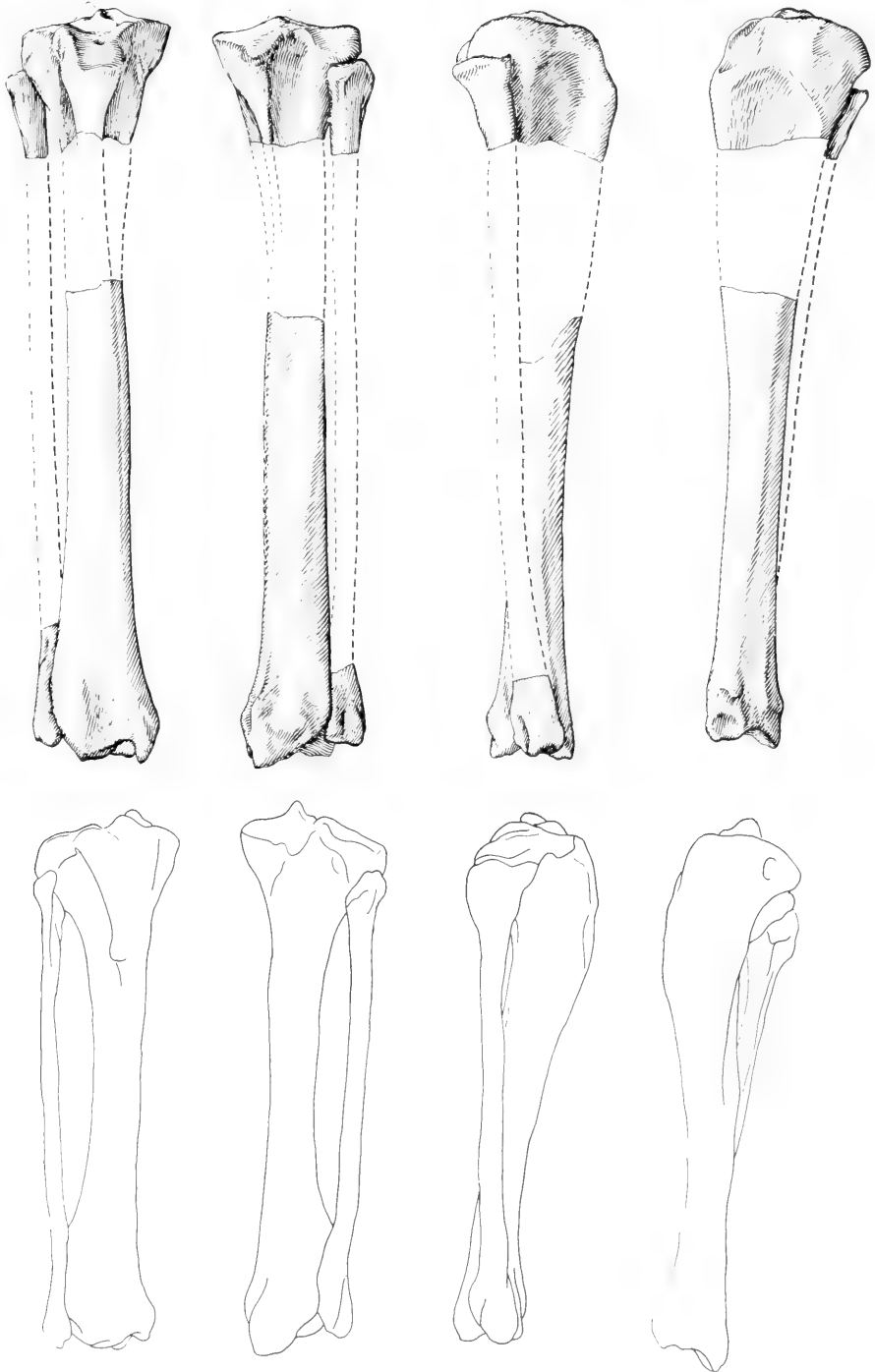
Fig. 17. Right tibia and fibula. Above, *Heptodon posticus,* MCZ 17670, in, from left to right, anterior, posterior, lateral and medial views. × ½. Below, *Tapirus pinchaque,* MCZ:M 6037, in same views. × ¼.

MCZ 17670, but judging from its condition in *Heptodon calciculus* and *Hyrachyus*, it must have extended above the level of the head. The head is hemispherical and extends anteromedially on a relatively long and thin neck. (There may have been a small amount of post-mortem anterior displacement of the head in MCZ 17670.) The trochanteric ridge is fairly prominent, and extends distally almost to the level of the lesser trochanter. The lesser trochanter is located slightly less than one-third of the way down the shaft, and the large third trochanter is situated slightly lower on the opposite side. A supracondyloid fossa, marking the origin of the plantaris, is evident on the posterior side of the shaft above the condyles. At the distal end of the femur, the trochlea is relatively narrow and almost symmetrical. Medial and lateral epicondyles are low. Pits for the popliteus and extensor digitalis longus are present on the lateral epicondyle. Lateral and medial condyles are separated by a deep intercondyloid fossa.

The femur of *Tapirus* (see Fig. 16) differs from that of *Heptodon* mainly in being slightly more robust, with wider trochlea and condyles and more massive epicondyles (especially the lateral one). The lesser and third trochanters in *Tapirus* are located about one-third of the way down the shaft. These differences are probably accounted for mainly by the larger size of the modern tapir.

Tibia (Fig. 17): The tibia of *Heptodon posticus* preserved in MCZ 17670 is missing about one-quarter of the shaft and it is not possible to determine its length. In *H. calciculus* (AMNH 294) the tibia is about as long as the femur. The proximal end of the tibia is about as deep anteroposteriorly as it is wide. The spine, or intercondyloid eminence, is broken off. The cnemial crest is fairly prominent and bears a large depression proximally for the middle patellar ligament. At the distal end of the shaft the medial malleolus is prominent and bears a large smooth scar from attachment of the

medial ligament. Posterior to the medial malleolus is a groove for the tendon of the flexor digitalis longus. On the lateral side there is a facet for articulation with the distal end of the fibula. The articular grooves for the astragalus are relatively deep, with the medial one narrower than the lateral one.

The tibia of *Tapirus* differs from that of *Heptodon* mainly in being relatively slightly more robust, with relatively wider proximal and distal articular surfaces and a more laterally expanded tuberosity (at the head of the cnemial crest). These differences may be accounted for by the larger size of the modern tapir. The laterally expanded tuberosity provides a greater area for attachment of the lateral patellar ligament and the fascia lata. In *Tapirus* the medial intercondyloid tubercle is higher than the lateral one, the reverse of the condition in *Heptodon*. The same change in relative heights of these tubercles occurred in equoid evolution (Kitts, 1956, p. 26). Increase in height of the medial tubercle would help prevent lateral dislocation of the femur relative to the tibia and might be correlated

Fig. 18.   *Heptodon posticus.*   MCZ 17670.   Right tarsus and proximal portions of metatarsals.   × ½.
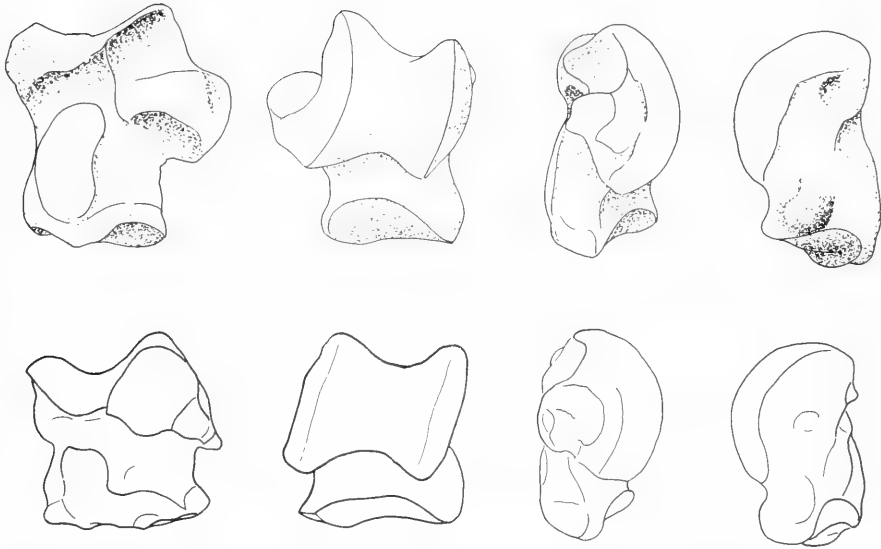
Fig. 19. Right astragalus. Above, *Heptodon posticus*, MCZ 17670, in, from left to right, posterior, anterior, lateral and medial views. Natural size. Below, *Tapirus pinchaque*, YPM 204, in same views. × ½.

with the relative increase in size of the lateral epicondyles (indicating more powerful extensor musculature) on femora of large perissodactyls.

Fibula (Fig. 17): Proximal and distal ends of the fibula are present in MCZ 17670 and indicate a relatively thin but complete bone which articulated with, but was not fused to, the tibia. The proximal articular surface is elliptical in outline and horizontally oriented. The distal end is expanded and has a vertical groove in its posterolateral side for the tendon of the peroneus brevis (lateral digital extensor). Distally, the medial surface forms the lateral side of the lateral articular groove for the astragalus.

The fibula of *Tapirus* is similar to that of *Heptodon*, differing only in having an oblique facet for the proximal articulation with the tibia. The lateral condyle of the tibia entirely covers the head of the fibula in *Tapirus*, while in *Heptodon* it is partly exposed.

Tarsus (Fig. 18): Seen in anterior view the tarsus of *Heptodon* is relatively high and narrow. The astragalus rests on the cuboid posteriorly but anteriorly the two are separated by a small calcaneum-navicular articulation. The ectocuneiform extends further distally than the cuboid or mesocuneiform so that it articulates with second and fourth metatarsals as well as the third.

In *Heptodon posticus* the trochlea of the astragalus (see Fig. 19) is about as high as it is wide, and has a relatively broad, shallow median groove. In *H. calciculus* the trochlea is relatively higher and narrower. The neck is relatively long and diverges slightly from the line of the trochlear crests. On the posterior (plantar) side of the astragalus the two main faces of the proximal calcaneal articulation are approximately perpendicular to each other. The sustentacular facet is relatively long and slightly proximodistally convex. The distal calcaneal facet is a long, low strip which in MCZ 17670 (*H. posticus*) does not, but in AMNH 294 (*H. calciculus*) does, contact the sustentacular facet. On the distal end of the astragalus the navicular facet is slightly wider than long, and is convex anteroposteriorly and slightly concave mediolaterally.
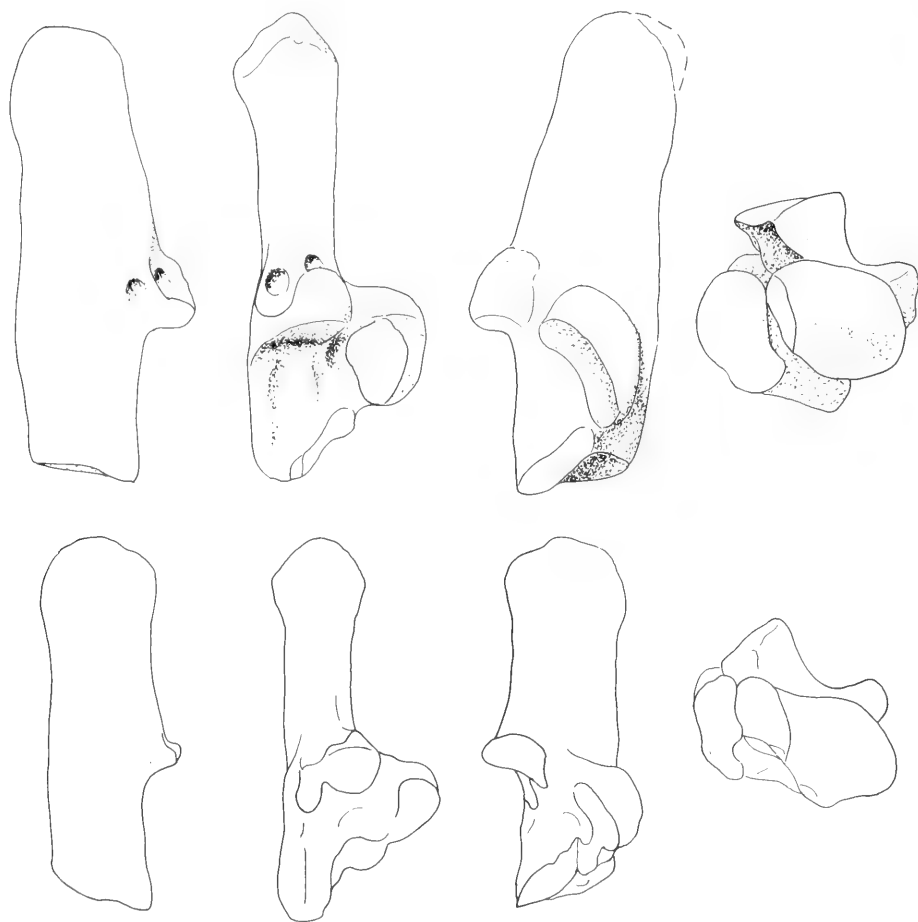
Fig. 20. Right calcaneum and astragalus. Above, *Heptodon posticus*, MCZ 17670, in, from left to right, lateral, anterior and medial views of calcaneum and distal view of astragalus and calcaneum. Natural size. Below, *Tapirus pinchaque*, YPM 204, in same views. × ½.

The cuboid facet is a relatively narrow, laterodistally-facing strip and does not reach the anterior edge of the astragalus. On the lateral side of the trochlea a broad pit marks the insertion of the short lateral ligament. On the medial side a shallow proximal pit indicates the insertion of the short medial ligament, while a tuberosity at the distal end of the neck marks the attachment area of the dorsal ligament.

The calcaneum (see Fig. 20) is relatively long and thin, with the lateral astragalar facet located slightly closer to the distal than proximal end. The tuber calcis is mediolaterally compressed and slightly expanded at its free end. The two major planes of the lateral astragalar facet meet at a right angle. A prominent pit just above this facet accommodated the distal end of the fibula in extreme flexion of the tibiotarsal joint. The sustentaculum is slightly higher than wide and bears an irregularly oval, slightly concave facet for the astragalus. A long, low facet on the distal end of the medial side of the body articulates with the navicular anteriorly and with the astrag-
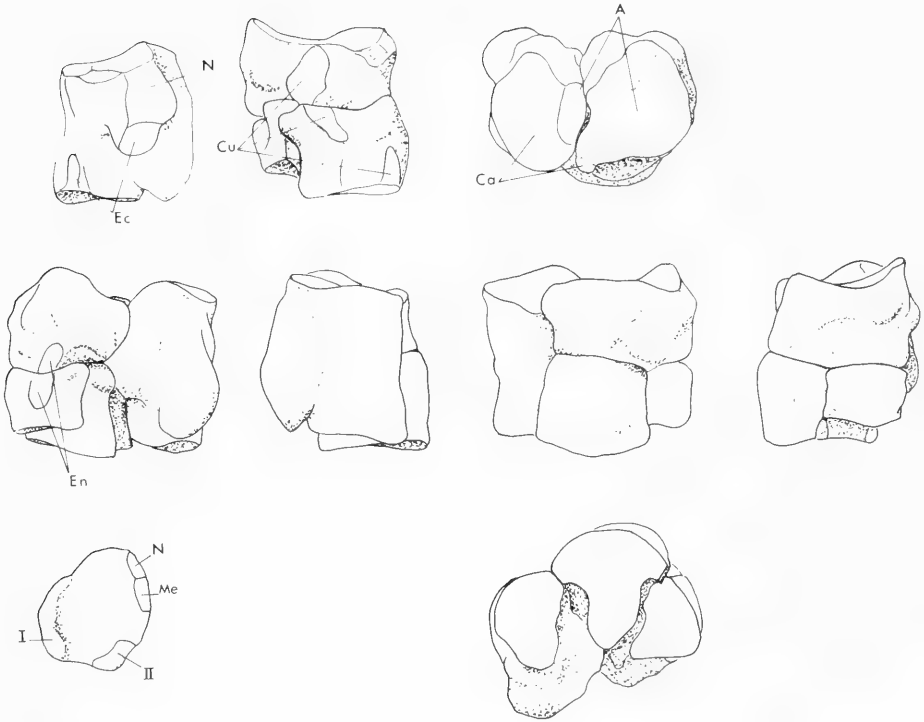
Fig. 21. *Heptodon posticus*. MCZ 17670. Right distal tarsals. Top row: (from left to right) cuboid, medial view; navicular, ecto- and mesocuneiforms, lateral view; cuboid and navicular, proximal view. Middle row: distal tarsals in, from left to right, posterior, lateral, anterior and medial views. Bottom row: entocuneiform in anterolateral view and cuboid, ecto- and mesocuneiforms in distal view. All natural size. Letters indicate articular contacts.

alus for most of its length. An irregularly oval, saddle-shaped cuboid facet occupies the entire distal end of the calcaneum. A pit on the lateral side of the calcaneum at the level of the lateral astragalar facet presumably marks the insertion of part of the short lateral ligament.

The cuboid (see Fig. 21) is relatively high and narrow, with a moderately large posterior tuberosity. The saddle-shaped calcaneal facet shares the proximal surface with a small elongate astragalar facet which does not reach the front of the cuboid. The proximal half of the medial side of the cuboid bears a small anterior facet and a large slightly concave posterior facet for the navicular. Just below the latter is a medio-distally inclined facet for the ectocuneiform. There is also a small anterior facet for the

ectocuneiform. The facet for the fourth metatarsal covers the distal surface.

The navicular is about as wide as it is deep (anteroposteriorly) with a saddle-shaped proximal surface for articulation with the astragalus. A small oblique facet at the anterolateral corner articulated with the calcaneum. The lateral side bears a large, gently convex posterior facet and a small anterior facet for the cuboid. On the posterior side there is a posterodorsally-facing facet for the entocuneiform. The distal surface bears a large triangular facet for the ectocuneiform and a small, roughly quadrangular facet for the mesocuneiform.

The ectocuneiform is triangular in proximal view and slightly higher than the navicular. In the articulated tarsus it extends further distally than the cuboid or meso-
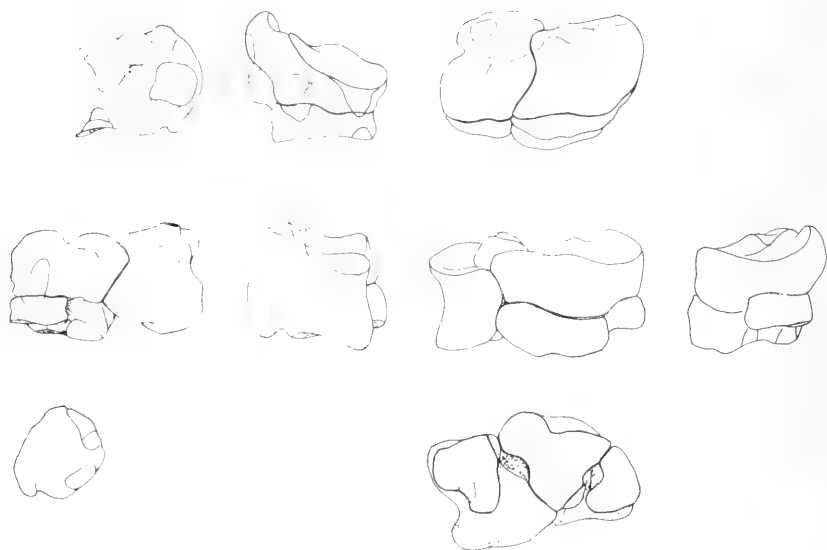
Fig. 22. *Tapirus pinchaque.* YPM 204. Right distal tarsals. Compare with Fig. 21. × ½.

cuneiform and has small distal facets on medial and lateral sides for the second and fourth metatarsals, respectively. It has a vertical anterior facet and a proximolaterally-facing posterior facet on the lateral side for articulation with the cuboid, and a large proximal facet for the mesocuneiform on the medial side. Distally, the ectocuneiform articulates with the third metatarsal by a relatively flat facet.

The mesocuneiform is small and roughly triangular in horizontal section. On its lateral side it has a proximal facet for the ectocuneiform and on its medial side a large proximal facet for the entocuneiform.

The entocuneiform and vestigial first metatarsal were briefly described in a previous paper (Radinsky, 1963b). The entocuneiform is roughly circular in posterior view, and relatively flat and anteroposteriorly compressed. On its anteromedial edge it bears adjacent facets for the navicular and mesocuneiform, and a short distance distally from these, a long facet for the second metatarsal. On the anterolateral edge there is an elongate prominence which articulated with the vestigial first metatarsal.

Metatarsals: The vestigial first meta-

tarsal is roughly oval and flat in posteromedial view, with a raised area on the lateral end of the anterior side. It bridged the gap between the lateral edge of the entocuneiform and the back of the head of the third metatarsal, articulating with the latter by a large facet. The contact with the entocuneiform left no facet.

Only the proximal ends of the second, third, and fourth metatarsals are preserved. The configuration of their proximal facets complements that of the distal facets of the distal tarsals (see Fig. 21) and need not be described here.

The pes of *Tapirus* (see Figs. 19–22) differs from that of *Heptodon* in the following features: astragalus relatively lower and wider, lacking a flange on the distal end of the lateral side of the trochlea; astragalo-navicular and astragalo-cuboid articulations relatively shorter (anteroposteriorly) and wider, and the latter more horizontal; proximal astragalo-calcaneal articulation shallower, with a lower proximal face; distal astragalo-calcaneal facet relatively higher and bent slightly; calcaneum lacking a pit above the proximal calcaneal-astragalar facet for the fibula, and with a
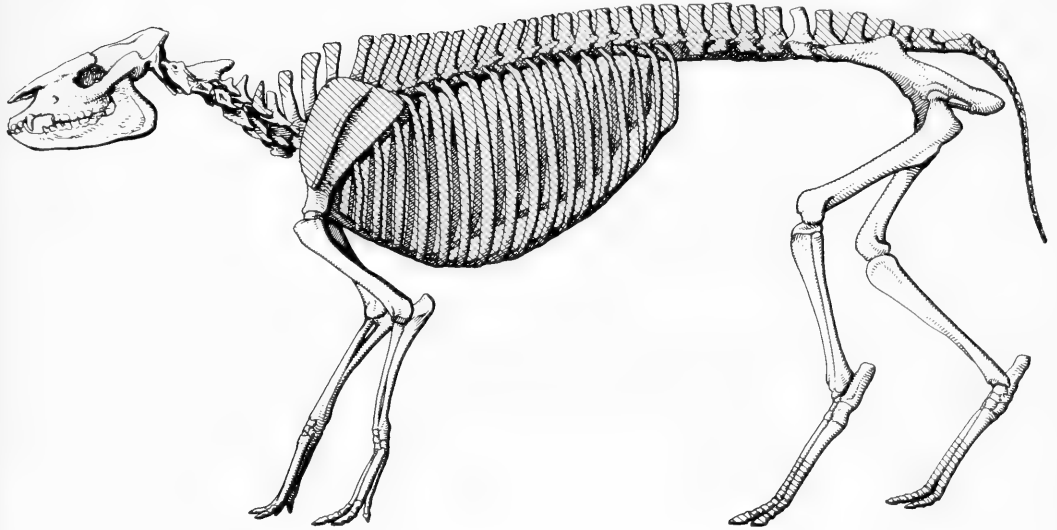
Fig. 23. *Heptodon posticus.* MCZ 17670. Skeleton in lateral view to show general proportions. Restored portions indicated by hatching. Slightly less than 1/4 size.

much shallower pit for the short lateral ligament; calcaneo-cuboid articulation relatively narrower; no calcaneo-navicular contact; cuboid relatively lower and longer (anteroposteriorly); anterior cuboid-navicular contact relatively larger; articulation between cuboid and fourth metatarsal more saddle-shaped and less flat; navicular relatively lower; ectocuneiform relatively lower and wider, without the small proximal posterior tuberosity seen in *Heptodon*; ectocuneiform-mesocuneiform articulation relatively smaller; mesocuneiform relatively lower and narrower, lacking a small proximal posterior tuberosity; entocuneiform more elongate. Metatarsals presumably relatively shorter and wider.

The differences listed above result in a relatively lower and wider tarsus in *Tapirus*, presumably in correlation with its heavier weight, compared to *Heptodon*. The absence of a pit on the calcaneum to receive the fibula in extreme flexion, and the lack of a flange on the astragalus for the fibula in extreme extension, suggests that a lesser degree of extension and flexion occurs at the tibiotarsal joint in *Tapirus* than it did in *Heptodon*.

CONCLUSIONS

The most striking osteological changes which occurred during fifty million years of evolution from *Heptodon* to *Tapirus* are modifications of the skull correlated with development of a proboscis. Primary changes were a tremendous enlargement of the nasal incision and a shortening of the nasals. These, in turn, caused several secondary changes. There were also less drastic cranial modifications which resulted from dental and brain evolution. By the end of the Oligocene, over 25 million years ago, the evolutionary changes which resulted in the modern tapirid skull were essentially completed, and there has been little cranial evolution in the Tapiridae since then.

The postcranial skeleton of *Tapirus* has remained basically similar to that of *Heptodon*, and most of the differences observed are correlated with the larger size of *Tapirus*. These differences include relatively broader and more robust limb bones and vertebrae, a less flexible vertebral column, and a much more expanded iliac blade in *Tapirus*.

Apparently, at some point in evolution

from *Heptodon* to *Tapirus*, there was a trend toward increasing cursorial specialization. This is indicated by such features in *Tapirus* as the reduction of the acromion of the scapula (correlated with loss of the clavicle), a widened lateral condyle on the humerus, the fusion of radius and ulna, and a relatively wider and shorter radio-carpal articulation than in *Heptodon*. However, modern tapirs are relatively heavy-bodied and short-legged, which suggests a more recent emphasis on large size, rather than speed, for defense against predators.

It is significant that the cursorial modifications mentioned above are confined to the fore limb; the same is true in other tapiroid lineages descended from *Heptodon*. This fact suggests that the hind limb of *Heptodon* was more specialized than the fore limb and had in fact approached its biomechanical limit of specialization for running (except for lengthening of distal limb segments in some tapiroid lineages). Thus, further modifications for running would be more likely to appear in the less specialized front limb.

ABBREVIATIONS

A	astragalus
aac	anterior opening of alisphenoid canal
alf	anterior lacerate foramen
C	cuneiform
Ca	calcaneum
Cu	cuboid
Ec	ectocuneiform
ef	ethmoid foramen
En	entocuneiform
feo	fenestra ovalis
fo	foramen ovale
fr	fenestra rotunda
ga	groove for artery
gav	groove for auricular branch of vagus
gct	groove for chorda tympani
gfn	groove for facial nerve
hf	hypoglossal foramen
iof	infraorbital foramen
L	lunar
M	magnum
Me	mesocuneiform
mf	maxillary foramen
mlf	middle lacerate foramen
N	navicular

of	optic foramen
ofc	opening of facial canal
P	pisiform
pac	posterior opening of alisphenoid canal
pgf	postglenoid foramen
plf	posterior lacerate foramen
pp	paroccipital process
ppf	posterior palatine foramen
ptp	post-tympanic process
R	radius
S	scaphoid
scf	sinus canal foramen
sf	stylomastoid foramen
spf	sphenopalatine foramen
T	trapezoid
Tm	trapezium
tt	ventral edge of tegmen tympani
ty	tympanic
U	unciform
Ul	ulna
I–V	metapodials

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Plate 1. *Heptodon posticus.* MCZ 17670. Lateral view of skull and mandible. Slightly less than natural size.
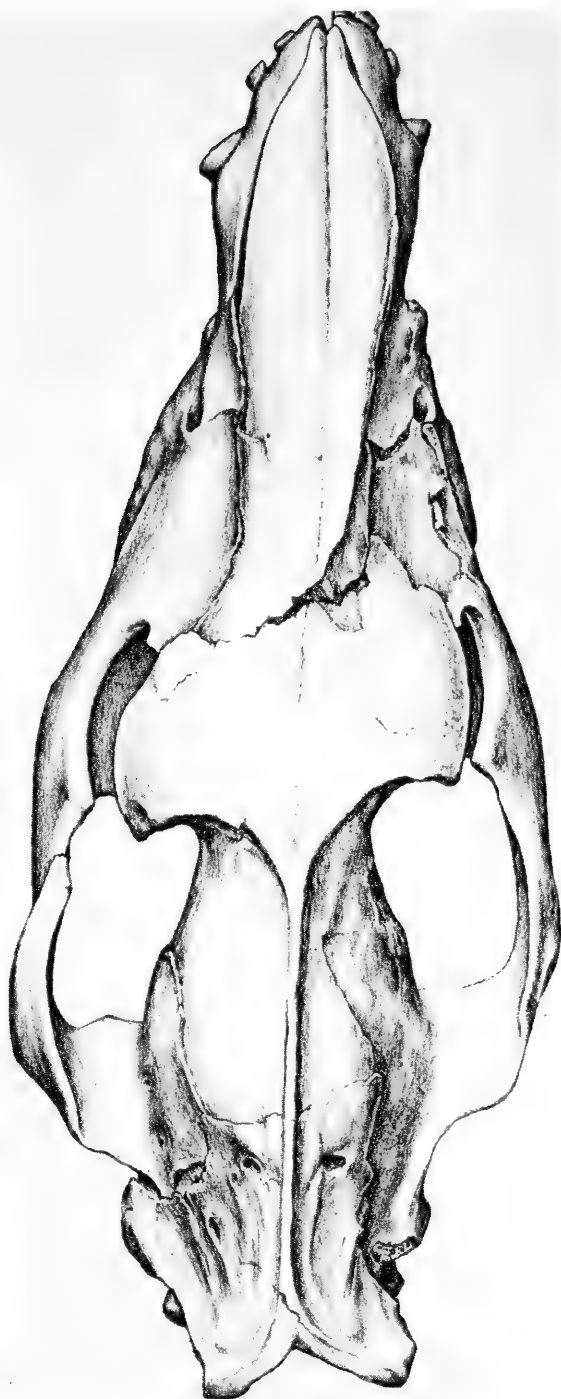
Plate 2. *Heptodon posticus.* MCZ 17670. Dorsal view of skull. Slightly less than natural size.
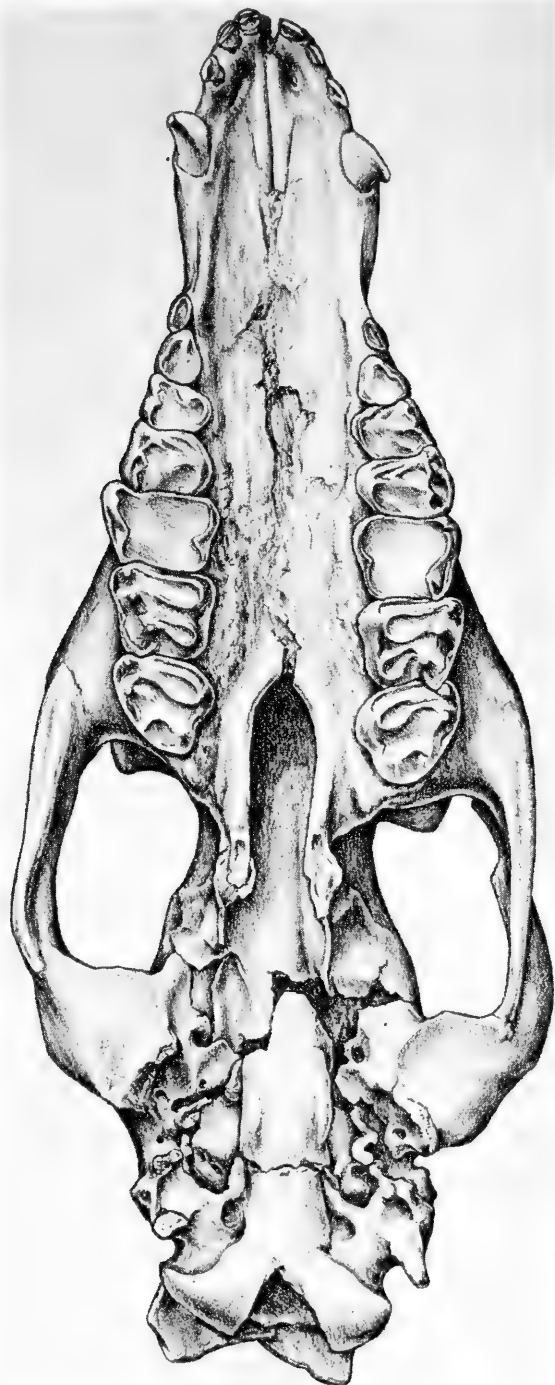
Plate 3. *Heptodon posticus.* MCZ 17670. Ventral view of skull. Slightly less than natural size.

The Species *Bufo granulosus* Spix (Salientia: Bufonidae) and its Geographic Variation

by JOSÉ M. GALLARDO

Museo Argentino de Ciencias Naturales "Bernadino Rivadavia,"
Buenos Aires, Argentina

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THE SPECIES *BUFO GRANULOSUS* SPIX (SALIENTIA: BUFONIDAE) AND ITS GEOGRAPHIC VARIATION

JOSÉ M. GALLARDO

INTRODUCTION

The present paper is part of a general study of the neotropical Bufonidae. In an earlier paper (1957) I discussed *Bufo granulosus* Spix and its distribution in Argentina; I now consider it in its entire range. Through the kindness of the authorities of several North and South American and European museums, I have examined 813 specimens; those studied in my earlier work bring the total to 1,198 specimens. I have thus been able to see a large proportion of the specimens cited in the literature, including types, paratypes, and topotypes. The materials studied belong to the following institutions, listed in order of abbreviation: American Museum of Natural History, New York (AMNH); The Academy of Natural Sciences of Philadelphia (ANSP); British Museum (Natural History), London (BMNH); Carnegie Museum, Pittsburgh (CM); Chicago Natural History Museum (CNHM); Instituto e Museo di Zoologia della Universita di Torino (IMZUT); Institut Royal des Sciences Naturelles de Belgique, Brussels (IRSN); Museo Argentino de Ciencias Naturales, Buenos Aires (MACN); Museo Civico di Storia Naturale "G. Doria," Genoa (MCSN); Museum of Comparative Zoology, Cambridge (MCZ); Muséum National d'Histoire Naturelle, Paris (MNHN); Museum of Vertebrate Zoology, University of California, Berkeley (MVZ); Museum of Zoology of the University of Michigan, Ann Arbor (MZUM); Rijksmu-seum van Natuurlijke Historie, Leiden (RNH); Senckenberg Museum, Frankfurt (SM); Facultad de Ciencias, Universidad Central de Venezuela, Caracas (UCV); United States National Museum, Washington (USNM); Zootomiska Institutet (University of Stockholm) (ZIUS); Zoologische Museum Berlin (ZMB); Zoologische Sammlung des bayerischen Staates, Munich (ZSBS). The gathering together and examination of these very large collections at the Museum of Comparative Zoology—at one time and in one place—has enabled me to reach new decisions.

HISTORICAL SUMMARY

The history of the classification of this species can be summarized as follows:

Spix (1824: 49, pl. 19, fig. 1, and 51, pl. 21, fig. 2) described the species under two different names, *Bufo globulosus* and *Bufo granulosus* (basing both names on specimens from the state of Bahia, Brasil). The vicissitudes of these two names and final prevalence of the second over the first may be followed in my earlier work on the species (Gallardo, 1957: 338–340).

Seventeen years later, Duméril and Bibron (1841: 697–698) described a toad from Uruguay under the name *Bufo dorbignyi*. When specimens from northern Brasil are compared with this one from Uruguay they prove to be quite different, especially with regard to the cephalic crests, low in the former and enormous in the latter. For this reason the two forms were considered

different species for many years. However, as more material has brought increase in knowledge of the amphibians of South America, *Bufo granulosus* and *B. dorbignyi* were cited randomly from localities between the type localities of the two taxa. Parker (1935: 509), studying specimens of *B. granulosus* from British Guiana, considered it probable that *B. dorbignyi* was only a subspecies of *B. granulosus*, since, according to him, the two intergraded in the Asunción region (Paraguay). Following this idea, Müller and Hellmich (1936: 7–14, fig. 3) recognized three subspecies of *B. granulosus*: *B. g. granulosus*, *B. g. major* and *B. g. dorbignyi*. Subsequently, most authors have considered *B. dorbignyi* as a subspecies of *B. granulosus*. Other authors reported differences, possibly of subspecific rank, between specimens of *B. granulosus* from different localities. Thus, Schmidt and Inger (1951: 444) observed that specimens from the state of Amazonas in Brasil have smooth crests, while those from Ceará, Paraíba, and Rio Grande do Norte have denticulate crests. Myers and Carvalho (1952: 1) considered it probable that several subspecies of *B. granulosus* may be differentiated. They cited differences between some localities in Brasil: for example, specimens from Araguaia (Rio Tapirapé) have a "flattened muzzle," differing from others from Pirapora (Minas Gerais), while a third type was found in Manáos and Santarém. Similarly, examples from São Luiz de Cáceres with "shortened physiognomy and strong infranarial crest," are close to others from Asunción (Paraguay). Myers and Carvalho have also described a species from the state of Rio de Janeiro, *Bufo pygmaeus*, which they considered close to *B. granulosus*.

In my earlier work (1957) I recognized three forms in Argentina: *B. g. dorbignyi*, *B. g. fernandezae* and *B. g. major*. After studying much more material, I have changed my concept of the typical subspecies *B. g. granulosus* (1957: 366–368) which I supposed would reach northern Paraguay;

actually what occurs in this region is *B. g. major*, while *B. g. mirandaribeiroi* subsp. nov. occurs in central Brasil, *B. g. granulosus* being restricted to northeastern Brasil.

As I stated for the Pseudidae (Gallardo, 1961), one can see in *B. granulosus* a clear distribution of the subspecies according to the hydrographical systems, a distinct subspecies belonging to the basin of each of the following rivers: Magdalena, Orinoco, Upper and Middle Amazon, Tocantins and Araguaia, São Francisco, Rio de la Plata. Because of this there are on occasion at nearly the same geographical latitude and a few kilometers apart two or three different subspecies, corresponding to different hydrographical systems; this occurs, for example, in Mato Grosso. Other subspecies belong to zones between basins or at the edge of the large basins; thus, distinct subspecies occur in a part of Uruguay and in southern Brasil, in the Chaco, in northwestern Bolivia, in northeastern Brasil, and in the Guianas. Some islands, such as Margarita Island near the Venezuelan coast, have their own subspecies; in others, such as Trinidad, the same subspecies exists as in the Orinoco basin.

SYSTEMATIC DESCRIPTIONS

Bufo granulosus Spix

Description of the species as a whole. Nostrils prominent. Supraorbital, preorbital, postorbital, suborbital, orbitotympanic, parietal, subnasal, canthal, and maxillary cephalic crests more or less well developed (in some subspecies very little developed and sometimes one or more absent); the crests may be granular, rippled or with smooth border according to the subspecies. The maxillary crest is smooth-bordered in all subspecies. The width of the interorbital space varies directly with the development of the supraorbital crest. Tympanum elliptic with the larger diameter dorsoventral, two-thirds the larger diameter of the eye. In some subspecies the tympanum is not very evident. First finger shorter than the second; subarticular tubercles double, especially evident on second

and third fingers; edge of fingers granulate, except the distal extreme. Palms with granulations usually conical, sometimes rounded; outer metacarpal tubercle large and irregularly round, inner tubercle small and elliptic. Hind limbs short, the tibio-tarsal articulation reaching shoulder or tympanum. First and second toes very short; double subarticular tubercles on the fourth toe; interdigital membrane reaching the toe tips, except in the fourth toe where it is present only at the base but is prolonged as a serrated cutaneous fringe to the tip; outer metatarsal tubercle not so prominent as the innermost, both conical, oblique. No tarsal fold, sometimes a line of spinous granules. Parotoids in general not very prominent, with lower edge not very evident; their lateral granules conical, the dorsal ones conical or rounded according to the subspecies. Granulations of the dorsum varying in shape in the subspecies, but in general the anterior are rounded, the lateral and posterior ones conical. Conical granulations on the limbs. Ventral skin with granules, smaller and abundant anteriorly, larger and sparser posteriorly.

Dorsum yellowish or greenish, with large dark spots. A vertebral light line exists in some subspecies but is absent in others. Belly yellowish.

Secondary sexual characters: males with one subgular medial vocal sac and darker skin in this region; first and second fingers dorsally brown (sometimes also the inner metacarpal tubercle). Females larger and with gular and pectoral granulations with small horny points.

Characters for the differentiation of the subspecies. In distinguishing the subspecies of *B. granulosus*, I found the following characters especially useful: the shape of the head; the degree of obliquity of the loreal region; the development of the snout; the shape of the rostrum, vertical or oblique; the position of the nostrils; the development of the cephalic crests, the characteristics of each crest, especially the maxillary and suborbital crests; the width, depth and

Map 1. Approximate ranges of the subspecies of *Bufo granulosus*: 1. *B. g. humboldti*; 2. *B. g. barbouri*; 3. *B. g. beebei*; 4. *B. g. merianae*; 5. *B. g. goeldii*; 6. *B. g. minor*; 7. *B. g. mirandaribeiroi*; 8. *B. g. lutzi*; 9. *B. g. granulosus*; 10. *B. g. major*; 11. *B. g. azarai*; 12. *B. g. fernandezae*; 13. *B. g. pygmaeus*; 14. *B. g. dorbignyi*.

granulations of the interorbital space; tympanum more or less evident, the plane of slope of the tympanum; the prominence of the parotoids and the type of their dorsal granulations; the presence or absence of a row of granules on the inner tarsal edge; and the presence or absence of the vertebral line. For certain determination of the subspecies it is necessary to take into consideration all these characteristics.

Distribution of the species. Bufo granulosus extends from Rio Calobre in Panama, to the Sierra de la Ventana, Buenos Aires Province, Argentina. It occurs in Colombia, Venezuela, Margarita and Trinidad islands, British and Dutch Guianas, Brasil (in all of its territory), northeast Peru, non-Andean Bolivia, Paraguay, Uruguay and Argentina

(Chacoan region, Mesopotamia, Santa Fé and Buenos Aires Province). Noticeable in this distribution is its absence in western South America; it has never been reported from Ecuador (though perhaps it exists in the Amazonian eastern part of that country), nor in most of Peru, in western Bolivia, in Chile, nor in western and southern Argentina. It does not extend as far to the west as *B. typhonius*, which has a wider distribution from Panama to Bolivia and from the Guianas and Brasil to Ecuador and Peru. In Argentina (Gallardo, 1957: 337), *B. granulosus* does not extend as far west and south as *B. arenarum*, which is a species very closely related to *B. rufus* of Minas Gerais (Brasil) and to *B. poeppigei* of eastern Peru.

Bufo granulosus granulosus Spix

Bufo granulosus Spix, 1824, p. 51, pl. 21, fig. 2 (type locality, Bahia); Martius, 1840, p. 27, pl. 21, fig. 2; Günther, 1858, p. 67 (part), pl. V, fig. A; Peters, 1873, p. 225; Boulenger, 1882, p. 324 (part); de Witte, 1930, p. 229; Schubart, 1939, p. 56; Schmidt and Inger, 1951, p. 444 (part).

Bufo globulosus Spix, 1824, p. 46, pl. 19, fig. 1 (type locality, Rio Itapicurú); Martius, 1840, p. 25, pl. 19, fig. 1; Peters, 1873, p. 223; Lutz, 1934, p. 124 (part), est. XXVII, fig. 6; Miranda Ribeiro, 1937, p. 56; Carvalho, 1937, p. 12.

Description. Adult male, USNM 97107, state of Bahia, Brasil. Head short, wide and high; loreal region nearly vertical. Snout short, though in ventral view the muzzle appears to project. Rostrum nearly vertical, but slightly sloping. Nostrils elongate, in some oblique. Cephalic crests low, with granular or scalloped border, except the maxillary crests which have smooth borders. Subnasals scarcely visible. Canthals visible, with granular borders. Suborbitals very near the lower edge of eye, not prolonged beyond the postorbitals. Preorbital crests well defined. Postorbital crests well defined, close to the anterior border of the tympanum and sloping anteriorly. Maxillary crests not expanded laterally; when the head is viewed dorsally, they are hidden by the suborbitals, and in ventral view there is not a conspicuous maxillary rim. Supraorbital crests low, the interorbital space slightly concave and granular. Parietal crests scarcely or not marked. Orbitotympanic crests present, but not well marked. Tympanum distinct, sloping outward. Parotoids not prominent, 9.5 mm long, with rounded dorsal granulations. One row of spinous granules on the tarsal internal edge.

Dorsal coloration. Orange with a black reticulum, interscapular space generally lighter but without well-defined vertebral light line (only a longitudinal medial groove). Belly yellowish.

Dimensions (in mm). Head and body 55. Head length 13. Head width 18. Head height 7. Eye 5. Interorbital space 6. Upper eyelid width 4. Elbow to third finger 23. Femur 19. Tibia length 19. Tibia width 6. Heel to fourth toe 28. Foot 12. Female, USNM 97109, same locality, head and body 56 mm.

Variation. In large animals the crests are continuous and with irregular borders. Canthal crests may be absent (a specimen from Baixa Verde, Rio Grande do Norte). Parietal crests present or absent. Subarticular tubercles of hand and foot sometimes simple.

Distribution. This form was described by Spix (1824) from the Rio Itapicurú and Bahia (state of Bahia, Brasil); its range is northeast Brasil: Itaeté, Joazeiro, Bonfim (Bahia), Tapera, Bonito (Pernambuco), Independencia (Paraíba), Natal, Ceará Mirim, Baixa Verde (Rio Grande do Norte).

Remarks. The types of *B. globulosus* and *B. granulosus* in the Zoologische Sammlung des bayerischen Staates in Munich were destroyed during World War II, according to a letter from Dr. W. Hellmich.

Literature citations referred to this subspecies. Günther (1858: 67), Pernambuco; Boulenger (1882: 324), Pernambuco only [I have seen BMNH 1881-7.4.8, Forbes coll.]; de Witte (1930: 229), Itaeté, Bahia [IRSN 71, examined]; Lutz (1934: 124), only Natal, Rio Grande do Norte; Schubart (1939: 56), localities in Pernambuco;

Schmidt and Inger (1951: 444), specimens from Paraíba and Rio Grande do Norte, probably also those from Ceará [material examined: CNHM 64198–210]; Cochran (1955: 24–25), specimens from Bahia, Pernambuco, Rio Grande do Norte, probably also those from Ceará [some of these specimens examined].

The specimens reported as *Bufo globulosus* by Miranda Ribeiro (1937: 56) and Carvalho (1937: 12) also belong to the present subspecies.

Material studied. **Brasil.** *Bahia.* Itaeté, IRSN 71 (3 specimens). Bonfim, CM 2650. Joazeiro, MZUM 108914 (1 specimen), USNM 98839. Estado de Bahia, USNM 97107–9. *Pernambuco.* Tapera, MCZ 15368. Bonito, MCZ 2059. Pernambuco, CNHM 42204, BMNH 1881 7.4.8, USNM 57877. Estado Pernambuco, MCZ 1502. *Paraíba.* Independencia, CNHM 64198–9. *Rio Grande do Norte.* Natal, USNM 81140, MZUM 74326. Ceará Mirim, CNHM 64201–10. Baixa Verde, CNHM 64200.

Bufo granulosus goeldii subsp. nov.

Bufo granulosus Cope, 1874, p. 120; Schmidt and Inger, 1951, p. 444 (part); Myers and Carvalho, 1952, p. 1 (part).

Holotype. MZUM 64528, adult male, Santarém, Pará, Brasil.

Paratypes. MZUM 122431–34, 4 males, same data; MCZ 353, female, also Santarém.

Description of type. Head short, wide and high; loreal region nearly vertical. Snout very short, but prominent. Rostrum nearly vertical. Nostrils elongate and oblique. Cephalic crests medium in development, generally with borders between smooth and rippled. Canthal crests with smooth borders. Subnasal crests distinct and with smooth borders. Suborbital crests little separated from the lower margin of the eye, some laterally expanded and not reaching beyond the postorbitals. Preorbitals oblique from front to rear. Postorbital crests near the anterior tympanic border and sloping forward. Maxillary crests with smooth borders, somewhat expanded laterally; in dorsal view the maxillary crests projecting

somewhat laterally; in ventral view they are seen as a distinct rim. Supraorbital crests not very high, interorbital space not very wide, with but little concavity and with short divergent crests at the canthal apex, medially smoother, posteriorly with small granules. Parietal crests marked. Orbitotympanic crests present and well marked. Tympanum sloping outward. Parotoids not prominent, length 8 mm, dorsal granules rounded. Granulations on dorsum few and small. One row of spinous granules on the inner tarsal edge. No vertebral light line, instead long oblique light and dark spots. Belly light yellowish.

Dimensions of type (in mm). Head and body 55. Head length 14. Head width 19. Head height 8. Eye 6. Interorbital space 7. Upper eyelid width 4. Elbow to third finger 23. Femur 21. Tibia length 19. Tibia width 6. Heel to fourth toe 29. Foot 19. Female paratype, MCZ 353, head and body 65 mm.

Variations. Sometimes no parietal crests or canthal crests, or suborbital crests not well marked. At the boundary of the subspecies area there are some forms transitional to other subspecies. Thus the Villa Murtinho specimens show a tendency towards *B. g. major*. In some specimens there is a partial vertebral line anteriorly. In juveniles the cephalic crests are more granular. Size range: males 40.5–55 mm; females 46.5–65 mm.

Distribution. *B. g. goeldii* extends over a large part of the Amazonas basin, from Santarém to the Upper Amazonas. It is known in Brasil from Santarém, Tapajóz, Obidos (state of Pará), Manáos, Lago Aleixo, Itacoatiara, Bôa Hora (state of Amazonas), Villa Murtinho, Pôrto Velho (Guaporé Territory), and in Peru from the Rio Marañón. To the Southwest it meets *B. g. minor* and *B. g. major*.

Remarks. I name this subspecies in honor of Dr. E. A. Goeldi, student of the Amazonas fauna.

Literature citations referred to this subspecies. Cope (1874: 120), Rio Marañón,

Peru [material examined ANSP 14257, MCZ 4773]; Schmidt and Inger (1951: 444), Itacoatiara, state of Amazonas [material examined: CNHM 64184–97, 64211–14]; Myers and Carvalho (1952: 1), Manáos, Santarém; Cochran (1955: 24), Pôrto Velho [material examined: MZUM 56777].

Material studied. **Brasil.** *Amazonas.* Santarém, MZUM 64528 (5 specimens), BMNH 1896.6.29.7–11, MCZ 353 (2 specimens), MCZ 400. Tapajóz, ANSP 25229, MCZ 1627 (5 specimens). Obidos, Rio Trombetas, MZUM 80402, MZUM 48295. Itacoatiara, CNHM 64184–97, 64211–14. Manáos, MCZ 1257. Bôa Hora, MZUM 57600. Pôrto Velho, MZUM 56763, 56768–9, MZUM 56773, 56777, 56778 (10 specimens). Villa Murtinho, MZUM 56764–67, 76078. Lago Aleixo, MCZ 17670. **Peru.** "Peru," ANSP 14257, MCZ 4773.

Bufo granulosus merianae subsp. nov.

Bufo granulosus Günther, 1858, p. 142; Boulenger, 1882, p. 324 (part); Van Lidth de Jeude, 1904, p. 93; Tate, 1932, p. 244.

Bufo globulosus Parker, 1935, p. 509.

Bufo strumosus Duméril and Bibron, 1841, p. 716 (part).

Holotype. AMNH 46531, adult male, head falls of Essequebo River, British Guiana.

Paratypes. AMNH 46525–30 + 10 specimens, same data.

Description of type. Head short, expanded laterally, high; loreal region nearly vertical. Snout short, but prominent. Rostrum nearly vertical. Nostrils elongate and somewhat oblique. Cephalic crests projecting, generally with rippled borders. Canthal crests marked, with smooth borders. Subnasal crests visible. Suborbital crests with little separation from the lower border of the eye, prolonged beyond the postorbital crests. Preorbital and postorbital crests together with the supraorbitals make a projecting rim around the eyes; the preorbitals slope to the rear; postorbitals near the anterior border of the tympanum. Maxillary crests with smooth borders, somewhat expanded in dorsal view; suborbital crests

projecting laterally; in ventral view the maxillary crests appear as a rim. Supraorbital crests projecting and rippled, with short oblique crests in the interorbital space; interorbital space concave, and granular, with the short divergent crests of the canthal apex hardly visible. Parietal crests scarcely marked. Orbitotympanic crests marked. Tympanum nearly vertical. Parotoids large, but not very prominent, length 10 mm; dorsal granulations rounded. One row of spinous granules on the inner tarsal edge. No vertebral light line; general coloration yellowish with long black spots. Ventral region gray-yellowish with dark spots.

Dimensions of type (in mm). Head and body 54. Head length 14. Head width 19. Head height 8. Eye 6. Interorbital space 9. Upper eyelid width 4. Elbow to third finger 24. Femur 17. Tibia length 17. Tibia width 7. Heel to fourth toe 28. Foot 19. Female paratype, AMNH 46525, head and body 70 mm.

Variations. Sometimes the parietal crests are well marked. The postorbital crests are far from anterior border of tympanum, especially in small animals. The vertebral light line is sometimes scarcely marked, in others distinctly visible. Sometimes there is a characteristic dorsal dark pattern: a reverse V between shoulders, a sacral rectangle, a supracloacal M and a circle upon each thigh. Ventrally, wholly light or with some dark spots. The specimens from near Mount Roraima show some differences: large and prominent reddish parotoids; wide dorsal black bands; ventrally many dark spots forming a reticulum. Size range: males 32.5–59.5 mm; females 36–72 mm.

Juvenile characters. Cephalic crests granular. Dorsum gray with well-defined darker spots; interocular, three spots between shoulders, one latero-abdominal and a supracloacal triangle; limbs striped. Belly spotted.

Distribution. British Guiana (head falls of Essequebo River, Rupununi River and Savannah, Isheartun, Wismar) and Surinam

(King Frederick William Falls, Saramacca, Zanderij). It also occurs in the adjacent region of Brasil (Paulo near Mount Roraima, Pacaraima, San José, Roraima) and Venezuela (Arabupu, Santa Elena, Cuquenán).

Remarks. I name this subspecies in honor of Marie Sybille Merian for her work on the Surinam fauna (1771).

Literature citations referred to this subspecies. Duméril and Bibron (1841: 718), Guiana, Cayenne ("*Bufo strumosus*"); Günther (1858: 142), Surinam; Boulenger (1882: 324), Surinam [material examined: BMNH 1858.11.25.153]; Van Lidth de Jeude (1904: 93), Lower Nickeri, Surinam [probable; not seen]; Parker (1935: 509), Rupununi, Savannah and Pacaraima foothills, British Guiana ("*Bufo globulosus*") [material examined: BMNH 1933.6.19.33–35; the marked development of the crests in this subspecies resembles that of *B. g. fernandezae* and *B. g. dorbignyi* and this character probably influenced Parker to suggest that *B. dorbignyi* was a subspecies of *granulosus*]; Cochran (1955: 25), Mount Roraima ("*B. g. granulosus*").

Material studied. **Brasil.** San José, AMNH 49383–4. Mt. Roraima, AMNH 3750. **British Guiana.** Paulo, Mt. Roraima, AMNH 39739–50, 39754, 39760. Pacaraima foothills, BMNH 1933.6.19.35. Head falls of Essequebo River, AMNH 46525–31. Rupununi River, AMNH 46484–93 (29 specimens). Upper Rupununi River, AMNH 46446–50. Rupununi Savannah, BMNH 1933.6.19.33–4. Wismar, AMNH 45761. Isheartun, AMNH 44544. King Frederick William Falls, BMNH 1936.9.3.19–20. **Surinam.** King Frederick William Falls, CNHM 30911. Near Saramacca River, kilometer 91.5, BMNH 1946.4.1.82–89. Zanderij, BMNH 1946.4.2.88, 92, 98, BMNH 1946.4.2.1–3 and 1946.4.1.90–91, 93–97. "Surinam," ANSP 2632–3. "Dutch Guiana," BMNH 1858.11.25.153. **Venezuela.** Arabupu, MZUM 85132–35 (13 specimens). Santa Elena, MZUM 85131. Seven miles fom Cuquenán, MZUM 85130.

Bufo granulosus minor subsp. nov.

Bufo granulosus Boulenger, 1898a, p. 5.

Holotype. MCZ 10089, adult male, Upper Beni below mouth of Mapiri, Bolivia.

Paratypes. MCZ 10090, same data; MZUM 57592 (15 specimens), same locality.

Description of type. Head short, wide and high; loreal region somewhat concave. Snout short, but prominent. Rostrum nearly vertical. Nostrils elongate, somewhat oblique. Cephalic crests somewhat projecting, generally with rippled borders. Canthal crests with smooth borders. Subnasal crests present and projecting. Suborbital crests close to the lower margin of the eye, not reaching beyond the postorbitals. Preorbitals and postorbital crests somewhat projecting; postorbital crests close to the tympanum. Maxillary crests with smooth borders, somewhat expanded; in dorsal view the maxillary crests project laterally; ventrally the maxillary crests appear as a rim. Supraorbital crests slightly projecting, interorbital space concave, with small divergent crests in the canthal apex and with granules in the parietal region. Parietal crests marked. Orbitotympanic crests marked. Tympanum nearly vertical. Parotoids prominent, but with lateral border not well marked, length 8 mm; dorsal granules rounded and horny. A row of spinous granules on the inner tarsal edge.

No vertebral light line. Dorsum brown, with light interorbital space and with a light triangle between shoulders and sacral region. Belly light.

Dimensions of type (in mm). Head and body 50. Head length 12. Head width 16. Head height 6. Eye 5. Interorbital space 6. Upper eyelid width 3. Elbow to third finger 22. Femur 15. Tibia length 13. Tibia width 6. Heel to fourth toe 26. Foot 17. Female paratype, MZUM 57592, head and body 51 mm, same locality as type. Size range: males 36–50 mm; females 39.5–51 mm.

Distribution. *B. g. minor* occurs in northern Bolivia in the Upper Beni River region:

Reyes, Rurrenabaque, Cachuela Esperanza and Muyurina, below the mouth of the Mapiri River. It adjoins *B. g. major*, with which it has some characteristics in common.

Remarks. The name of this subspecies is given on account of its small size, contrasting with *B. g. major*, geographically close but of large size in general, as indicated by the name.

Literature citations referred to this subspecies. Boulenger (1898a: 5), various localities in Bolivia, i.e., Reyes, Santa Ana de Marinos, Missiones Mositenes. [I have seen specimens only from the first locality (MCSN 29800) but probably those from the other localities mentioned belong to this subspecies.]

Material studied. **Bolivia.** Santa Cruz, Muyurina, USNM 142103–4; Upper Beni, below mouth of Rio Mapiri, MZUM 57588, 57592, 57595 (21 specimens), MCZ 10089–90; Reyes, right bank of Beni River, MCSN 29800 (2 specimens); Rurrenabaque, MZUM 57587, 57589, 57594 (12 specimens); Cachuela Esperanza, MZUM 57593 (5 specimens).

Bufo granulosus beebei subsp. nov.

Bufo granulosus Ruthven, 1922, p. 55 (part); Lutz, 1928, p. 89, est. 16, figs. 5–6; Parker, 1933, p. 11; 1936, p. 1; Beebe, 1952, p. 174; Lynn, 1959, p. 113.

Bufo globulosus Lutz, 1927, p. 42, est. 8, figs. 5–6; 1934, p. 124 (part), est. XXV.

Holotype. AMNH 55774, adult male, Churchill-Roosevelt Hwy., Trinidad, B.W.I.

Paratypes. AMNH 55771, 55773, 55775 + 8 duplicate specimens, same data.

Description of type. Head elongate, not wide, depressed; general body shape pyriform. Loreal region oblique. Snout elongate. Rostrum sloping. Nostrils elongate and oblique. Cephalic crests not very prominent with smooth or somewhat rippled borders. Canthal crests with smooth borders. Subnasal crests indistinct. Suborbital crests close to the lower border of the eye, continued just beyond the postorbitals by granules. Preorbital crests projecting, forming a small flange in front of the eyes, sloping to

the rear. Postorbital crests close to the anterior border of the tympanum and sloping in front. Maxillary crests with smooth borders, scarcely expanded; in dorsal view the suborbitals project somewhat laterally; ventrally, the maxillary crests appear as a narrow rim. Supraorbital crests but little raised, with short divergent crests on the parietal region; interorbital space somewhat concave, with granules and small divergent crests in the canthal apex. Parietal crests visible, but very short. Orbitotympanic crests well marked. Tympanum slightly sloping outward. Parotoids large, length 8.5 mm; dorsal granules large, rounded and flat. One row of spinous granules on the inner tarsal edge.

Vertebral light line absent or just visible anteriorly. General color light brown, with two reversed dark V's on the dorsal medial line, the more anterior one forming an "X" with the parietal crests. Limbs transversely striped. Belly light, with indistinct dark spots.

Dimensions of type (in mm). Head and body 43. Head length 11. Head width 15. Head height 5. Eye 4. Interorbital space 6. Upper eyelid width 3. Elbow to third finger 19. Femur 14. Tibia length 15. Tibia width 5. Heel to fourth toe 23. Foot 15. Female paratype, AMNH 55771, head and body 48 mm.

Variation. There is one specimen transitional to *B. g. humboldti*, with short snout, from Sucre, Venezuela. (It is on the basis of this specimen that I regard *beebei* as a subspecies of *B. granulosus*.) In some specimens there is a very slender vertebral line; in others it is partly or wholly absent. The ventral region may be light or with small dark spots. Size range: generally of small size, males 35.5–51 mm, females 47–53 mm.

Distribution. Along the Rio Orinoco basin, in Venezuela (San Fernando de Atabapo, Upper Orinoco, Puerto Ayacucho, Maracay, Urugen); it occurs also in Falcon and Sucre states (Cumanacoa). It is also recorded by specimens from Gaira (Colom-

bia), and Trinidad (San Rafael, St. Augustine, Churchill-Roosevelt Hwy.).

Remarks. I name this subspecies after Dr. William Beebe, explorer of Trinidad.

Literature citations referred to this subspecies. Lutz (1927: 42, pl. 8, figs. 5–6; 1928: 89, pl. 16, figs. 5–6; 1934: 124, pl. 25), Maracay, Venezuela [I have seen USNM 97193–5]; Cochran (1955: 25); Parker (1933: 11), Trinidad; Beebe (1952: 174), Arima Valley, Trinidad; Lynn (1959: 113), St. Augustine, Trinidad; Parker (1936: 1), Upper Orinoco, Venezuela [material examined: IRSN 71].

Material studied. **Venezuela.** *Terr. Fed. Amazonas.* Upper Orinoco, IRSN 71 (2 specimens), UCV 13, 28–29, 41–47. San Fernando de Atabapo, MCZ 27825. Puerto Ayacucho, Rio Orinoco, AMNH 23220–1. *Bolivar.* Urugen, UVC 3166. *Aragua.* Maracay, USNM 97193–5. *Sucre.* Cumanacoa, CM 9028, 9054, 9096. *Falcon* ? "Venezuela," UCV (15 specimens). **Colombia.** Gaira, MZUM 45527. **Trinidad.** "Trinidad," CNHM 43667. St. Augustine, MCZ 19889 (2 specimens). San Rafael, CNHM 49603–4. Churchill-Roosevelt Hwy., AMNH 55770–78 (29 specimens).

Bufo granulosus barbouri subsp. nov.

Bufo granulosus Brongersma, 1948, p. 90, fig. 30.

Holotype. RNH 10867, adult male, Porlamar, Isla Margarita, V-25-1936.

Paratypes. RNH 10868, same data, 1 female and 9 males.

Description of type. Head moderately elongate, somewhat wide, depressed; body wide. Loreal region slightly sloping, with small broken crests. Snout prominent, short and wide. Rostrum somewhat sloping. Nostrils elongate and oblique. Cephalic crests somewhat elevated and in general with lightly rippled borders. Canthal crests with smooth borders. Subnasal crests visible. Suborbital crests near lower border of the eye, reaching a little beyond the postorbitals. Preorbital crests not very salient, sloping posteriorly. Postorbital crests separated from the tympanum. Maxillary crests with smooth borders, but little expanded; in dorsal view, the suborbital crests projecting laterally; ventrally the maxillary crests appear as a narrow rim. Supraorbital crests little salient, with small divergent crests in the parietal region; interorbital space slightly concave and granular, with small divergent crests in the canthal apex. Parietal crests poorly marked. Orbitotympanic crests visible, but not expanded. Plane of the tympanum gently sloping. Parotoids not prominent, length 10.5 mm; dorsally with small conical granules. A poorly marked row of granules on tarsus.

Vertebral light line absent, but a light triangle between shoulder and sacral region; with dark)(-shaped spots between shoulders, and a sacral M-shaped spot. Belly light.

Dimensions of type (in mm). Head and body 55. Head length 14. Head width 19. Head height 8. Eye 5. Interorbital space 6. Upper eyelid width 4. Elbow to third finger 24. Femur 19. Tibia length 18. Tibia width 6. Heel to fourth toe 29. Foot 20. Female paratype, RNH 10868, same locality, head and body 59 mm. Size range in males 54.5–55 mm, in females 57.5–59 mm.

Juvenile characteristics. Cephalic crests granular.

Distribution. Margarita Island (Guantamare, Porlamar, La Asunción).

Remarks. I name this subspecies in honor of the late Dr. T. Barbour, former Director of the Museum of Comparative Zoology.

Additional material studied. **Venezuela.** *Margarita Island.* La Asunción, USNM 139066–8. Guantamare, RNH 10869 (14 specimens), Porlamar, RNH 10870 (28 specimens), 10871 (4 specimens), 10872 (2 specimens).

Bufo granulosus mirandaribeiroi subsp. nov.

Bufo granulosus Cott, 1926, p. 1159; Myers and Carvalho, 1952, p. 1 (part).

Bufo granulosus granulosus Gallardo, 1957, p. 367 (part).

Holotype. BMNH 1923.11.9.15, male adult, Marajó Island, mouth of Amazon.

Paratypes. BMNH 1923.11.9.16–19, same data.

Description of type. Head elongate, not wide behind the tympanum, depressed. Loreal region sloping and somewhat concave. Snout somewhat prominent and very broad, elongate and sharp. Rostrum sloping. Nostrils elongate and oblique. Cephalic crests smooth, not raised. Canthal crests marked. Subnasal crests visible, but not salient. Suborbital crests close to the lower border of the eye, not meeting postorbitals. Preorbital crests not raised, sloping to the rear. Postorbital crests not raised, near the tympanic anterior border and sloping to the front. Maxillary crests little expanded; in dorsal view the suborbital crests projecting laterally; ventrally, the maxillary crests appear as a narrow rim. Supraorbital crests little salient, with small divergent crests posteriorly; interorbital space somewhat concave, granular, and with small divergent crests on the canthal apex. Parietal crests little visible. Orbitotympanic crests present, but not expanded. Plane of tympanum gently sloping. Parotoids not well marked, length 9 mm; dorsal granules rounded. Dorsal body granules rather flat. Row of tarsal granules scarcely visible. A vertebral light line; general dorsal coloration brown and olive with dark, irregular spots. Belly light.

Dimensions of type (in mm). Head and body 51. Head length 12. Head width 16. Head height 5. Eye 5. Interorbital space 5. Upper eyelid width 4. Elbow to third finger 21. Femur 19. Tibia length 17. Tibia width 5. Heel to fourth toe 28. Foot 18. Female paratype, BMNH 1923.11.9.17, same locality; head and body 61 mm.

Variation. Sometimes suborbital crests somewhat prolonged behind postorbitals. In one specimen from Mato Grosso, vertebral light line not very well marked, very thin. Size range of males 50–52.5 mm, of females 47.5–62 mm.

Distribution. Along the Rio Tocantins and its tributary the Araguaia, on Soure (Marajó Island), on the Upper Araguaia

(Goyaz), Fazenda Montaría on the Rio Araguaia and on Commandante Rodon (Mato Grosso), all localities in Brasil.

Remarks. I name this subspecies in honor of A. Miranda Ribeiro for his work on the amphibians of Brasil.

Literature citations referred to this subspecies. Cott (1926: 1159), Marajó Island; Myers and Carvalho (1952: 1), Rio Tapirape, a tributary of the Araguaia; Cochran (1955: 24–25), Lower Amazonia (USNM 28932–7), and Soure, Marajó Island (AMNH 46196–7) [I have seen these], and also Fazenda Montaría [considered by me (Gallardo, 1957: 367) as probably *B. g. granulosus*].

Material studied. **Brasil.** *Pará.* Soure, on Marajó Island, mouth of Amazon River, AMNH 46196–7; Marajó Island, mouth of Amazon, BMNH 1923.11.9.15–19; "Lower Amazonia," USNM 28932–7. *Goyaz.* Upper Araguaia, USNM 130179–81. *Mato Grosso.* Fazenda Montaría, Rio Araguaia, MACN 2407 (3 specimens); Commandante Rodon, MCZ 15660.

Bufo granulosus lutzi subsp. nov.

Bufo granulosus Myers and Carvalho, 1952, p. 1 (part).

Bufo granulosus granulosus Cochran, 1955, p. 22 (part), pl. 3, fig. D.

Holotype. MZUM 108908, adult male, Pirapora, Minas Gerais, Brasil.

Paratypes. MZUM 122426–7, same data; MZUM 108912, Barreiras, Bahia, Brasil.

Description of type. Head moderately elongate, wide, depressed. Loreal region sloping and somewhat concave. Snout short, but prominent. Rostrum somewhat sloping. Nostrils elongate and oblique. Cephalic crests smooth and low, sometimes between granular and smooth. Canthal crests not well marked. Subnasal crests little marked. Suborbital crests near the lower border of the eye, not expanded and not meeting suborbitals and postorbitals. Preorbital and postorbital crests but little projecting; postorbital crests sloping forward and close to the anterior border of tympanum. Maxillary crests not expanded; in dorsal view, the sub-

orbital crests projecting laterally; ventrally, the maxillary crests appear as a narrow rim. Supraorbital crests low, without short divergent crests in the parietal region. Interorbital space somewhat concave, granular and without short divergent crests in the canthal apex. Parietal crests not well marked. Orbitotympanic crests not expanded. Plane of tympanum gently sloping. Parotoids somewhat prominent, length 8 mm; dorsal granules rounded. Row of tarsal granulations poorly marked. A vertebral light line; dorsum yellowish with dark longitudinal irregular bands. Belly light.

Dimensions of type (in mm). Head and body 50. Head length 12. Head width 16. Head height 6. Eye 4. Interorbital space 5. Upper eyelid width 4. Elbow to third finger 21. Femur 17. Tibia length 17. Tibia width 6. Heel to fourth toe 26. Foot 18. Female paratype, MZUM 108912, Barreiras, Bahia. Head and body 48 mm.

Variation. Sometimes vertebral light line absent or poorly marked. Size range of males 44–53 mm, of females 48–59 mm.

Juvenile characteristics. Crests granular. Two dark and broken reversed V's on the dorsal medial line. Ventrally with not well-marked dark spots or all light.

Distribution. Along the Rio São Francisco and affluents, excepting the mouth of this river, where *B. g. granulosus* occurs; on Toca de Onça, Barreiras, Bom Jesus da Lapa, Barreiro on Rio Grande (Bahia), Remanso, Januária, São Francisco, Pirapora (Minas Gerais). Also probably in state of Ceará. All localities in Brasil.

Remarks. I name this subspecies in honor of Dr. A. Lutz for his work on the amphibians of Brasil.

Literature citations referred to this subspecies. Myers and Carvalho (1952: 1), Pirapora, Minas Gerais; Cochran (1952: 1), Pirapora (USNM 98244–6), Januária (USNM 98807–11), São Francisco (USNM 98805), all in Minas Gerais [I have seen this material].

Material studied. **Brasil.** *Bahia.* Toca da Onça, USNM 52613–4. Barreiro on Rio Grande, MZUM 108912–3. Bom Jesus da Lapa, MZUM 108902, 108910–11 (10 specimens). *Minas Gerais.* Remanso do Anacleto, MZUM 108909. Januária, MZUM 108905–7 (6 specimens), USNM 98807–11. São Francisco, USNM 98805. Pirapora, MZUM 108903–4, 108908 (5 specimens), USNM 98244–6. *Ceará.* "Ceara," MCZ 430. *State uncertain.* Amazon Valley, MCZ 10276.

Bufo granulosus humboldti subsp. nov.

Bufo granulosus Cope, 1899, p. 1; Ruthven, 1922, p. 55 (part); Noble, 1924, p. 66; Dunn, 1944, p. 513; Stebbins and Hendrickson, 1959, p. 514.

Holotype. MCZ 24882, adult male, Gualanday, W. of Girardot, Dept. Tolima, Colombia.

Paratype. MCZ 8978, female, Fundación, Colombia.

Description of type. Head short, wide near the eyes, high. Loreal region somewhat sloping. Snout short, but prominent. Rostrum nearly vertical. Nostrils elongate and oblique. Cephalic crests salient and with rippled borders. Canthal crests with smooth borders; a narrow intercanthal space. Subnasal crests scarcely visible. Suborbital crests near the lower border of the eye, expanded and somewhat prolonged beyond the postorbitals. Preorbital crests well marked, somewhat sloping posteriorly. Postorbital crests well marked, near the tympanic anterior border. Maxillary crests with smooth borders, not much expanded; in dorsal view, the suborbital crests projecting laterally; ventrally, the maxillary crests appear as a rather wide rim. Supraorbital crests somewhat projecting; interorbital space somewhat wide and concave, with granules, with very elevated canthal apex and with short divergent crests. Parietal crests hardly visible. Orbitotympanic crests expanded laterally. Tympanum gently sloping laterally and posteriorly. Parotoids subtriangular, not well marked, length 7 mm; with conical rounded dorsal granules. Row of tarsal spinous granules, not well marked. No vertebral light line; dorsum brown with large dark spots, with

a light triangle between shoulders and sacral region; limbs with transverse dark bands. Belly light yellowish.

Dimensions of type (in mm). Head and body 48. Head length 12. Head width 17. Head height 6. Eye 4. Interorbital space 5. Upper eyelid width 4. Elbow to third finger 19. Femur 15. Tibia length 15. Tibia width 5. Heel to fourth toe 26. Foot 17. Female paratype, MCZ 8978, Fundación, Colombia. Head and body 53 mm.

Variation. Rostrum sometimes somewhat sloping. Suborbital crests sometimes poorly marked or not well prolonged beyond postorbitals. Orbitotympanic crests laterally more or less expanded. In some specimens the vertebral light line scarcely visible. Ventral dark spots can be indistinct. Size range of males 35–59 mm, of females 53–63.5 mm.

Juvenile characteristics. Crests granular. Two reversed dark V's on the medial dorsal line, sometimes broken in the apex. Belly light.

Distribution. Panama (Rio Calobre, Isla de Barro Colorado, Arraiján), Colombia and part of Venezuela. In Colombia, it exists, in general, along the Rio Magdalena and also near the Sierra de Santa Marta; Villavieja, Cerbatana (Dept. Huila), Gualanday, Carmen de Apicalá, Mariquita, Honda (Dept. Tolima), Puerto Berrío (Dept. Antioquia), Rio Frío, Rio Cesar, Valledeupar, Fundación, Aracataca, Santa Marta, Valencia, Mamatoco, Curumaní (Dept. Magdalena), Sierra Maciuti (Dept. Guajira). But it also occurs to the east of the Cordillera Oriental in Colombia, in El Astillero (Dept. Norte de Santander) and Villavicencio (Dept. Meta), and in Venezuela near San Fernando de Atabapo (*B. g. beebei* also occurs at or near the last locality). Other localities from Venezuela are in general to the northwest of the Cordillera de Mérida: Cua, Lago de Maracaibo, Rio Guasare, El Paito (this last locality very near to Maracay, where *B. g. beebei* is found). Closer to the coast, in the Falcon State, *B. g. beebei* also occurs.

Remarks. Named in honor of the Baron A. von Humboldt for his explorations of South America.

Literature citations referred to this subspecies. Cope (1899: 1), probably from the neighborhood of Bogotá; Ruthven (1922: 55), Santa Marta, Fundación, Aracataca, Valencia, Valledeupar [I have seen these specimens which clearly belong to this subspecies, but the specimen from Gaira, Colombia, belongs to *B. g. beebei*]; Noble (1924: 66), Rio Calobre, Panama [material examined: USNM 53739]; Dunn (1944: 513) (considered one of the commonest toads in Colombia); Stebbins and Hendrickson (1959: 514), various Colombian localities [I have seen all their material].

Material studied. **Panama.** Rio Calobre, USNM 53739; Arraiján, ANSP 23391; Barro Colorado Island, Canal Zone, AMNH 22830. **Colombia.** "Colombia," AMNH 20358, 39090, 39127–8. *Guajira.* Sierra Maciuti, USNM 115380; Rio Cesar, USNM 117515. *Magdalena.* Santa Marta, MCZ 8977; Fundación, MCZ 8978, MZUM 45523, 48202–7, 48209 (12 specimens); Curumaní, MCZ 21499; Rio Frío, MCZ 16052, 16054; Aracataca, ANSP 19731; Valencia, Santa Marta Mts., MZUM 54637; Mamatoco, Santa Marta Mts., MZUM 45524, 45526, 48208; Valledeupar, Santa Marta Mts., MZUM 54635–6. *Antioquia.* Puerto Berrío, CNHM 30801–4 (5 specimens). *Tolima.* Mariquita, CNHM 81833–4. Gualanday, MZUM 90600 (2 specimens), MCZ 24882–4. Carmen de Apicalá, 400 m, MVZ 41993. Honda, MCZ 16264. *Huila.* Villavieja, 1400 feet, MVZ 63015–8, 63023–4, 5 km N. Villavieja, 1400 feet, MVZ 63019–22, 63025–7 (6 specimens), 6 km SE. Villavieja, 458 m, MVZ 41992 (2 specimens). *Norte de Santander.* El Astillero, Inst. La Salle 250b. **Venezuela.** Lago de Maracaibo, CNHM 3016 (2 specimens). *Aragua.* Cua, CNHM 69780. *Tachira.* Rio Guasare, UCV 3239. *Carabobo.* El Paito, Sur de Valencia, UCV 3167–70. *Territorio Amazonas.* San Fernando de Atabapo, UCV 3171.

Bufo granulosus major Müller and Hellmich

Bufo granulosus major Müller and Hellmich, 1936, pp. 12–13, fig. 3 (type locality San José de Chiquitos, Bolivia); Gallardo, 1957, pp. 364–366, pl. II, figs. 5–7, pl. III, fig. 10, pl. IV, fig. 13.

Bufo d'orbignyi Boettger, 1885, p. 246.

Bufo d'orbignyi Boettger, 1892, p. 39; Andersson, 1906, p. 14.

Bufo granulosus Boulenger, 1894, p. 348 (part); Budgett, 1899, p. 313; Müller and Hellmich, 1936, p. 7 (part); Travassos and Freitas, 1942, p. 283; B. Lutz, 1946, pp. 153, 154; Myers and Carvalho, 1952, p. 1 (part).

Bufo globulosus Berg, 1896, p. 198 (part).

Bufo granulosus d'orbignyi Vellard, 1948, pp. 143, 146; Cei, 1949, pp. 532, 541, 544, pls. I–II; 1950, p. 405 (part); 1953, pp. 512 (part), 515; 1955, p. 291; 1956a, pl. I, fig. 5.

Bufo granulosus granulosus Gallardo, 1957, pp. 366, 367, 368 (part).

Topotype. Adult male, ZSBS 202/26, San José de Chiquitos, Bolivia.

Description. Head short, wide at buccal commissure, high. Loreal region sloping. Snout short, but prominent. Rostrum nearly vertical. Nostrils elongate and oblique. Cephalic crests somewhat raised, with rippled borders, but almost all the lateral crests granular. Canthal crests with smooth borders, intercanthal space rather wide. Subnasal crests distinct and projecting, with smooth borders. Suborbital crests near the lower border of the eye, not laterally expanded, nor prolonged beyond postorbitals. Preorbital crests well marked, scarcely sloping posteriorly. Postorbital crests well marked, sloping a little anteriorly, close to the anterior border of the tympanum. Maxillary crests with smooth borders, laterally expanded, projecting in dorsal view. In ventral view, the maxillary crests appear as a wide rim. Supraorbital crests somewhat projecting; interorbital space concave and wide, granular and with the short divergent crests poorly marked. Parietal crests poorly marked. Orbitotympanic crests generally not well marked. Tympanum distinct, gently sloping. Parotoids thin with poorly marked borders, length 10 mm; dorsal granules conical and horny. A row of spinous granules on the inner tarsal edge. No vertebral light line; a dorsal dark reticulation. Belly yellowish, light.

Dimensions (in mm). Head and body 55.5. Head length 14. Head width 18. Head height 6. Eye 5. Interorbital space 6. Upper eyelid width 4. Elbow to third finger 23. Femur 20. Tibia length 18. Tibia width 7. Heel to fourth toe 31. Foot 21. Female topotype, ZSBS 202/26, head and body 64.5 mm.

Variation. The suborbital crests may be somewhat laterally expanded and prolonged beyond postorbitals; in this character there is a resemblance to *B. g. fernandezae*. Parietals sometimes scarcely visible. Parotoid dorsal granules rounded (only one specimen). Only one specimen with a vertebral light line. Size range in males 43–70 mm, in females 50–81 mm. Specimens from Puerto Casado (Paraguay), MACN 1756, and from northern Chaco (Paraguay), ZSBS 70/32, are of small size.

Distribution. All the Chacoan region, in Bolivia (San José de Chiquitos, Buenavista, Tatarenda, Ixiamas, Lago Rogagua), the Paraguayan Chaco (Puerto Vallemi, Puerto Casado, Colonia Mennonita), the Argentinian Chaco (Provinces of Salta, Formosa, Chaco, Santiago del Estero, Santa Fé) and in Brasil in the Pantanal zone of Mato Grosso (Miranda, Pôrto Esperança, Villa Maria, Salobra). In northern Bolivia it meets *B. g. minor* and *B. g. goeldii*. In Pôrto Esperança (Brasil) and in Puerto Casado (Paraguay) it meets *B. g. fernandezae* which extends to the south.

Literature citations referred to this subspecies. In addition to the type series (Müller and Hellmich, 1936: 12) and the material cited by me (Gallardo, 1957: 364) as *granulosus*, the following literature citations are referred to this subspecies:

Boettger (1885: 246; 1892: 39), Paraguay (*Bufo dorbignyi*) [I have now been able to examine these specimens, SM 3148, which I had earlier erroneously considered *B. g. fernandezae* (Gallardo, 1957: 347)]; Boulenger (1894: 348), Asunción, Para-

guay [only BMNH 1894.3.14.161–162, which are probably from the Paraguayan Chaco; two others reported from Asunción are *B. g. fernandezae*, and are probably correctly localized]; Berg (1896: 198), Corrientes, Argentina (*B. globulosus*) [material studied: MACN 3748]; Budgett (1899: 313), Paraguayan Chaco (*B. granulosus*); Andersson (1906: 14), Tatarenda, Bolivia (*B. dorbignyi*) [material studied: ZIUS]; Bertoni (1914: 21), Paraguay [probable]; Müller and Hellmich (1936: 7), San José de Chiquitos, Santa Cruz de la Sierra and northern Chaco [I have seen these, but specimens from San José, Formosa, are *B. g. fernandezae*]; Travassos and Freitas (1942: 283), Salobra, Mato Grosso (*B. granulosus*) [I have studied material from this locality]; B. Lutz (1946: 153, 154), Miranda, Mato Grosso (*B. granulosus*) [material studied: CNHM 67092–3]; Myers and Carvalho (1952: 1), São Luiz de Cáceres, Upper Paraguay River, specimens described as with "short physiognomy and strong infranarinal crest" [I have seen one specimen MCSN 29817, from Villa Maria, the same locality that is now called São Luiz de Cáceres]; Gallardo (1957: 366, 367, 368), Puerto Vallemi (MACN 2405–6), Puerto Casado, Paraguay (MACN 1756), referred to as "probably *B. g. granulosus*."

Material studied. **Paraguay.** "Paraguay," SM 3148. Asunción, BMNH 1894.-3.14.161–162. Colonia Mennonita, 22°10′S, 60°W, Chaco, BMNH 1956.1.2.8–9. Northern Chaco, ZSBS 70/32 (6 specimens). Estancia Guajhó, Puerto Casado, MACN 1756 (5 specimens). Puerto Vallemi, Departamento Concepción, MACN 2405–6. **Bolivia.** San José de Chiquitos, ZSBS 202/26 (3 specimens), CM 36217 (18 specimens), MCZ 29826–43. Buenavista, MCZ 15563 (2 specimens), CM 3824, 4236, MZUM 60548, 60549, 63329, 66522 (9 specimens). Tatarenda, Chaco boliviano, ZIUS (3 specimens). Ixiamas, MZUM 57596 (5 specimens). Lago Rogagua, MZUM 57590 (2 specimens). **Brasil.** *Mato Grosso.* Pôrto Esperança, MZUM 104284. Salobra,

USNM 132907–8, MZUM 104291, 104293. Miranda, MZUM 104289, CNHM 67092–3. Environs of Villa Maria, MCSN 29817. (Argentine specimens recorded in my previous paper are not cited here.)

Bufo granulosus azarai subsp. nov.

Holotype. Adult male, BMNH 1955.1.5.-47, Primavera, Upper Paraguay, Paraguay.

Paratypes. AMNH 19877–81, Paraguay.

Description of type. Head short, wide and very depressed. Loreal region sloping and concave. Snout very short, not projecting (hardly visible from the ventral side), but prominent. Rostrum nearly vertical. Nostrils elongate and oblique. Cephalic crests well developed, with smooth or somewhat rippled borders. Canthal crests with smooth borders. Subnasal crests distinct. Suborbital crests well separated from the lower border of the eye, forming a small projecting arch, expanded laterally and prolonged beyond postorbitals. Preorbital crests marked. Postorbital crests marked and somewhat separated from the tympanum. Maxillary crests very much expanded laterally; seen from above, the maxillaries project laterally; ventrally, the maxillaries appear as an expanded rim. Supraorbital crests projecting, with short divergent crests in the parietal region; interorbital space concave and very wide, granular and with short divergent crests on the canthal apex. Parietal crests marked. Orbitotympanic crests with thick border. Tympanum visible, gently sloping. Parotoids not prominent, length 7 mm; dorsally with flat granules. Granules on the dorsum rather smooth. The row of granules on the inner tarsal edge indistinct. A vertebral light line, thin and irregular; dorsal coloration generally dark gray or brown, with scattered, small darker spots. Belly with dark spots.

Dimensions of type (in mm). Head and body 50. Head length 11. Head width 15.5. Head height 5. Eye 3.5. Interorbital space 7. Upper eyelid width 3. Elbow to third finger 17. Femur 14. Tibia length 14. Tibia width 5. Heel to fourth toe 20. Foot 15.

Female paratype, AMNH 19878, Paraguay. Head and body 57 mm.

Variation. Seen from above, the suborbital crests sometimes project more than the maxillaries. Vertebral light line generally absent or only indicated. Ventrally sometimes without spots.

Juvenile characters. Granulated crests, not prominent, similar to those of juveniles in other subspecies. Dorsal coloration gray with darker spots in the shape of two broken inverse V's, on the dorsal median line.

Distribution. Near the rivers that begin in the Sierras de Maracajú and Amambay on the Paraguayan–Brasilian border; Primavera (24°30'S, 56°40'W,) in Paraguay and Maracajú (southern Mato Grosso) in Brasil. These Sierras make a "divortium aquarum" between the Paraná and Paraguay rivers. To the west of the locality of Maracajú, in Miranda, *B. g. major* occurs, while to the west of Primavera, *B. g. fernandezae* occurs on the banks of the Paraguay River.

Remarks. I name this subspecies in honor of the Spanish naturalist Felix de Azara, for his work on the fauna of Paraguay.

Material studied. **Paraguay.** Primavera, 24°30'S, 56°40'W, Alto Paraguay, BMNH 1955.1.5.45–47 (3 specimens); "Paraguay," AMNH 19877–81. **Brasil.** Mato Grosso. Maracajú, USNM 107701.

Bufo granulosus pygmaeus Myers and Carvalho

Bufo pygmaeus Myers and Carvalho, 1952, p. 1 (type locality São João da Barra, Estado de Rio de Janeiro, Brasil).

Description of paratype. USNM 132357, adult male, São João da Barra. Head moderately elongate, wide at the angle of the mouth, and depressed. Loreal region sloping. Snout short and prominent. Rostrum somewhat sloping backwards. Nostrils elongate and oblique. Cephalic crests with smooth or somewhat rippled borders. Subnasal crests distinct. Suborbital crests near the lower border of the eye, not much expanded laterally, prolonged beyond the postorbitals. Preorbital crests visible, sloping forward (not vertical) and far from the

anterior border of the tympanum. Maxillary crests scarcely expanded; in dorsal view the maxillaries project laterally; ventrally, the maxillaries appear as a somewhat expanded rim. Supraorbital crests somewhat raised; interorbital space somewhat concave and granular. Parietal crests marked. Orbitotympanic crests well marked. Plane of tympanum gently sloping. Parotoids not prominent, length 4 mm; dorsally with smooth granules. A row of tarsal granules not well marked. A vertebral light line; dorsally large dark and light spots. Belly light gray.

Dimensions of specimen described (in mm). Head and body 29. Head length 8. Head width 11. Head height 4. Eye 3. Interorbital space 3. Upper eyelid width 3. Elbow to the third finger 13. Femur 9. Tibia length 9. Tibia width 3. Heel to fourth toe 15.5. Foot 10.

Variation. Only one specimen without vertebral light line among thirteen examined. Five specimens with black ventral spots. Size range, according to Myers and Carvalho (1952: 2) of males 25–41 mm, of females 31–42 mm.

Distribution. Myers and Carvalho (1952: 1) say this form is distributed along the littoral region of the state of Rio de Janeiro (São João da Barra on the mouth of the Rio Parahyba and Restinga da Marambaia). The other subspecies geographically close are: *B. g. lutzi* to the north in Pirapora (Minas Gerais) and *B. g. dorbignyi* to the southwest in Alto de Serra (São Paulo).

Remarks. I believe this form can be considered as a subspecies of *B. granulosus* and that it is close to other subspecies occurring in eastern Brasil. I have studied 13 paratypes of this subspecies, but I have not seen the specimens which Cei (1956b: 324) reported from Ituzaingó, Corrientes, Argentina. I think it is probable that the latter are *B. g. fernandezae*, which has some characters in common with *pygmaeus* and sometimes is of small size.

Material studied. **Brasil.** *Rio de Janeiro.* São João da Barra, USNM 132356–7, MZUM 104960, 115657 (11 specimens).

Bufo granulosus fernandezae Gallardo

Bufo granulosus fernandezae Gallardo, 1957, pp. 347–358, pl. I, figs. 1, 2; pl. III, fig. 9; pl. IV, fig. 12; pl. V, figs. 14–16. (Type locality Bella Vista, Provincia de Buenos Aires, Argentina.)

Bufo granulosus Boulenger, 1889, p. 247; 1894, p. 348 (part); 1898b, p. 126; Peracca, 1895, p. 29; Müller and Hellmich, 1936, p. 7 (part); Gallardo, 1958, pp. 291, 298, 300.

Bufo d'orbignii Burmeister, 1861, vol. 1, p. 481; vol. 2, p. 533.

Bufo d'orbignyi Müller, 1882, p. 127 (part), p. 138 (part), p. 143; Fernandez, 1926, p. 308, pl. II, fig. 4; pl. III, fig. 4; pl. IV, fig. 1 (part), figs. 4–5; Cei, 1953, p. 521.

Bufo Dorbignyi Berg, 1896, pp. 151, 154, 196 (part).

Bufo granulosus d'orbignyi Cei, 1953, p. 521 (part); Cei and Pierotti, 1955, pp. 11, 12, 14; Ringuelet and Aramburu, 1957, p. 25 (part).

Description of type. MACN 10.334, adult male, Bella Vista, Provincia de Buenos Aires, Argentina. Head short, wide and high. Loreal region somewhat sloping. Snout short though somewhat projecting, prominent in ventral view. Rostrum nearly vertical. Nostrils elongate and little oblique. Cephalic crests high, with smooth borders or somewhat rippled. Canthal crests well developed. Subnasal crests distinct. Suborbital crests rather far from the lower border of the eye, expanded laterally and prolonged beyond the postorbitals. Preorbital and postorbital crests visible, but not very prominent; postorbital crests far from the lower border of the eye, expanded laterally and prolonged beyond the postorbitals. Preorbital and postorbital crests visible, but not very prominent; postorbital crests far from the anterior border of the typanum. Maxillary crests somewhat expanded; in dorsal view suborbital crests project laterally; ventrally, the maxillaries appear as a wide rim. Supraorbital crests developed, but not covering the upper eyelid; interorbital space somewhat concave and deep, somewhat granular. Parietals well marked. Orbitotympanic crests well developed. Tympanum visible, anterior border somewhat prominent, nearly vertical. Parotoids subtrian-gular, somewhat elongate (10 mm), lower border not well marked; dorsally with flat granules. No row of granules on the inner tarsal edge. Vertebral light line with an interscapular expansion; ground color blackish with greenish spots. Belly grayish yellow with dark spots.

Dimensions of type (in mm). Head and body 60. Head length 15.5. Head width 20. Head height 8. Interorbital space 5.5. Upper eyelid width 4. Elbow to third finger 25. Femur 21. Tibia length 19. Heel to fourth toe 32.5. Foot 22. Female paratype (allotype) MACN 10.355 same locality. Head and body 80 mm.

Variation. Parietal crests little marked or only one side marked. Suborbitals prolonged sometimes only on one side of the head. Specimens from Pôrto Esperança (where the subspecies meets *B. g. major*) without vertebral light line or with only the interscapular expansion. Size range of males 36–65 mm, females 68–80 mm.

Juvenile characters. Dorsum with five dark spots in pentagonal disposition. Belly light or with dark spots.

Distribution. Along the Paraguay, Paraná, Uruguay (Argentine side) and La Plata rivers, in general not far from the banks; thus from Pôrto Esperança in Mato Grosso (Brasil) and Puerto 14 de Mayo, Bahía Negra (Paraguay) to near La Plata, Province of Buenos Aires (Argentina). In Uruguay from Nueva Palmira to Montevideo.

Literature citations referred to this subspecies. Burmeister (1861, 1: 481, and 2: 533), Paraná, Entre Rios, Argentina (*B. dorbignyi*); Müller (1882:127, 138, 143), Leones, Córdoba, Argentina (*B. dorbignyi*) [I studied material from this locality for my earlier work]; Boulenger (1889: 247), Resistencia, Chaco, Argentina [material studied: MCSN 29611]; Boulenger (1894: 348), Asunción, Paraguay [material examined: BMNH 1894.3.14.159–160]; Boulenger (1898b: 126), Puerto 14 de Mayo, Paraguay [material examined: MCSN 30492]; Peracca (1895: 29), Resistencia, Argen-

tina. Asunción, Paraguay [material from Asunción studied: IMZUT 1084]; Berg (1896: 151, 154, 196), Corrientes, Santa Fé and Entre Rios, Argentina, and some of his specimens from Buenos Aires, Argentina, and from the Republica de Uruguay; Müller and Hellmich (1936: 7), San José, Formosa (*B. g. granulosus*) [material studied: ZSBS 152/28]; Cochran (1955: 26), La Plata (USNM 22750), Montevideo, Uruguay (USNM 65576, 70618) (*B. g. dorbignyi*) [USNM 70618 is one of the specimens reported by Metcalf (1940: 486, 487, 489, 563) as *B. dorbignyi*]; Cei and Pierotti (1955: 11, 12, 14), Paraná Delta; Gallardo (1958: 291, 298, 300), typical locality (a paper written before the subspecies was described).

Remarks. The intermediate position of this subspecies becomes evident from an analysis of its synonymy, since what the European authors generally reported as *B. granulosus* was, to Argentinians and Americans, *B. dorbignyi.*

Material studied. **Argentina.** "Provincia de Buenos Aires," AMNH 11962; La Plata, CNHM 9691–3, USNM 22750; Isla Ella, Rio Paraná, MZUM 76113; Gualeguaychú, Entre Rios, MACN 7114 (2 specimens); Colonia Resistencia, Chaco, MCSN 29611 (6 specimens), MCSN 29915; San José, Formosa, ZSBS 152/28 (18 specimens). **Uruguay.** Montevideo, MZUM 59011 (2 specimens), BMNH 1923.12.4.11–13, USNM 65576, 70618. **Paraguay.** "Paraguay," MCZ 2237; Rio Pilcomayo, CNHM 42294; Colonia Nueva Italia, CNHM 42295–7, AMNH 50672–5, MCZ 25801–3; Asunción, IMZUT 1084 (10 specimens), BMNH 1930.11.27.-293–7, 1894.3.14.159–160; Bahía Negra, Puerto 14 de Mayo, MCSN 30492. **Brasil.** Pôrto Esperança, Mato Grosso, MZUM 104271, 104283 (3 specimens).

Bufo granulosus dorbignyi Duméril and Bibron

Bufo d'Orbignyi Duméril and Bibron, 1841, p. 697 (type locality Montevideo); Hensel, 1867, p. 141; Müller, 1882, pp. 127, 138 (part); Boulenger, 1885b, p. 296; Nieden, 1923, pp. 76, 143 (part), fig. 191; Lutz, 1934, p. 123 (part), pl. XXVII, figs. 1–1a.
Bufo Orbignyi Bibron, 1847, p. 11.
Bufo D'Orbignyi Bibron, 1847, pl. 15, figs. 5–7; Marelli, 1931, p. 201 (part).
Bufo d'orbignyi Günther, 1858, p. 67 (part); Boulenger, 1882, pp. 285, 322, figs.; Baumann, 1912, pp. 143, 146, 154 (part); Miranda Ribeiro, 1926, p. 132 (part); Vanzolini, 1953, p. 125; Klingelhöffer and Scherpner, 1956, p. 160, fig. 127.
Bufo dorbignyi Cope, 1885, p. 185.
Bufo D'orbignyi Boulenger, 1885a, p. 196.
Bufo Dorbignyi Boulenger, 1886, pp. 442, 443; Berg, 1896, pp. 151, 154, 196 (part); Marelli, 1924, p. 586 (part); Mello-Leitão, 1937, p. 342 (part).
Chilophryne d'Orbignyi Fitzinger, 1843, p. 32.
Chilophryne d'orbignyi Cope, 1862, p. 358.
Chilophryne D'orbignyi Jiménez de la Espada, 1875, p. 188.
Bufo granulosus d'orbignyi Cei, 1953, pp. 512, 521 (part); Cochran, 1955, p. 25 (part), pl. 3, figs. G–I; pl. 34, fig. F; Gallardo, 1957, p. 358, pl. I, figs. 3–4; pl. III, fig. 8; pl. IV, fig. 11; Ringuelet and Aramburu, 1957, p. 25 (part).

Redescription of type. MNHN 4960, adult female, Montevideo, Uruguay. Head short, wide, and high. Loreal region nearly vertical. Snout very short, barely seen ventrally. Rostrum nearly vertical, rounded. Nostrils elongate and little oblique. Cephalic crests very high, with smooth or somewhat rippled borders. Canthal crests very high. Subnasal crests distinctly visible. Suborbital crests not marked. Preorbital crests well defined. Postorbital crests very poorly marked. Maxillary crests much expanded; in dorsal view the maxillaries project laterally; ventrally, the maxillaries appear as a very expanded rim. Supraorbital crests very well developed, covering laterally part of the upper eyelids resembling an extra eyelid; interorbital space very concave and deep, practically without granules. Parietals well marked. Orbitotympanic crests very high. Tympanum in general not well marked; nearly vertical. Parotoids subtriangular, with lower border not well marked, length 7 mm; dorsal granules flat. No row of granules on inner tarsal edge. A verte-
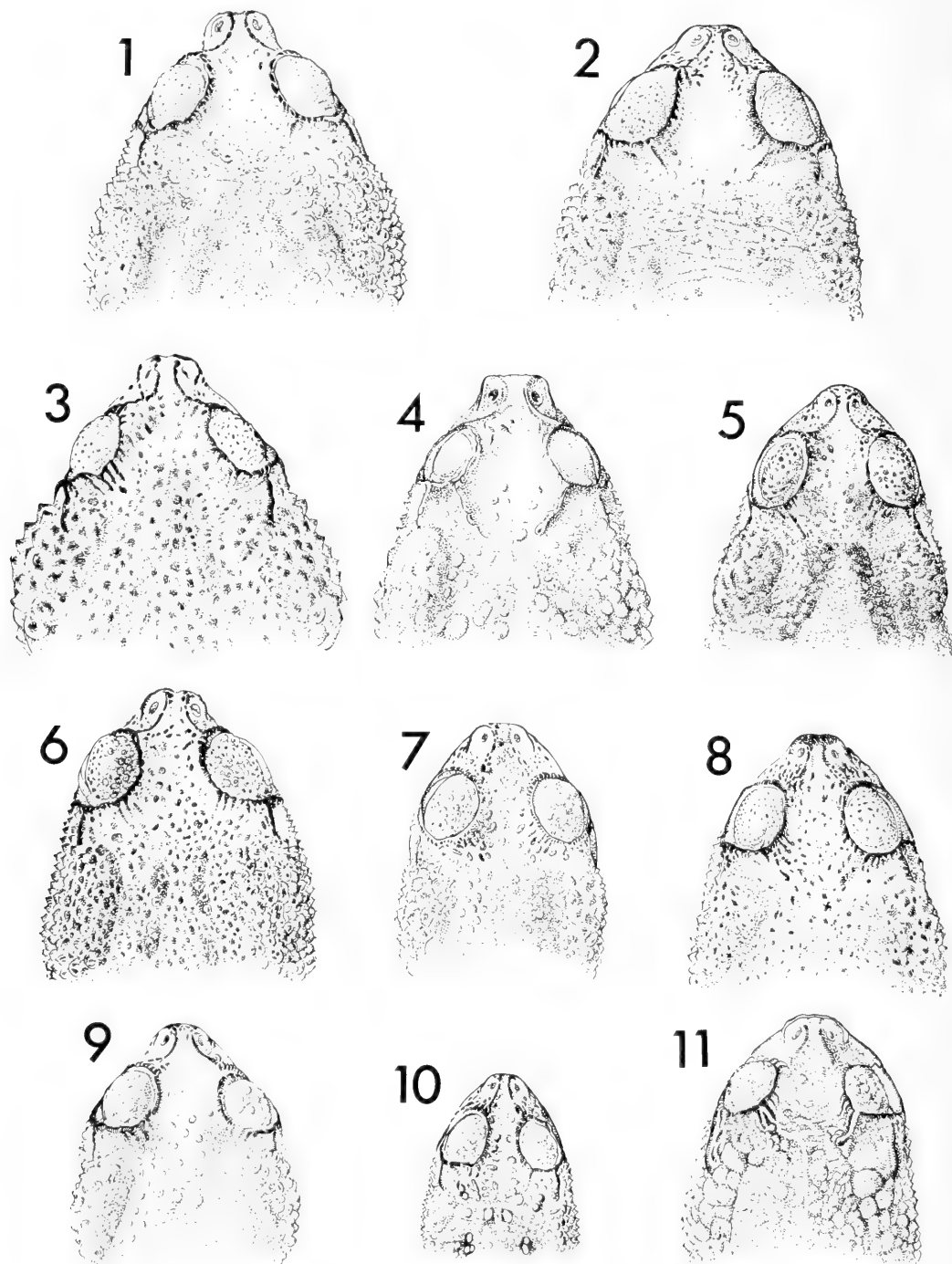
Fig. 1. Dorsal views of heads of *Bufo granulosus* subspecies. 1. *Bufo g. granulosus*, USNM 97107. 2. *B. g. goeldii*, MZUM 64528. 3. *B. g. merianae*, AMNH 46531. 4. *B. g. minor*, MCZ 10089. 5. *B. g. beebei*, AMNH 55774. 6. *B. g. barbouri*, RNH 10867. 7. *B. g. mirandaribeiroi*, BMNH 1923.11.9.15. 8. *B. g. lutzi*, MZUM 108908. 9. *B. g. humboldti*, MCZ 24882. 10. *B. g. pygmaeus*, USNM 132357. 11. *B. g. azarai*, BMNH 1955.1.5.47.

bral light line; dorsum with large dark spots; dark bands on limbs. Belly grayish yellow.

Dimensions (in mm). Head and body 66. Head length 14. Head width 21. Head height 7.5. Eye 5. Interorbital space 9. Upper eyelid width 3. Elbow to third finger 24. Femur 17. Tibia length 17.5. Tibia width 7. Heel to fourth toe 29.5. Foot 21.5.

Variation. Specimens from marginal zones of the subspecies area, as Pôrto Alegre and Montevideo, show some variation of the crests: supraorbitals rather low; parietals more or less distinct; suborbitals very variable: (a) only a feeble indication not prolonged behind postorbitals; (b) visible, separated from lower border of eye but neither expanded nor prolonged; (c) present, only prolonged on one side of head; maxillaries somewhat broken; postorbitals obscurely visible. Other variations are: tympanum very distinct (well separated from postorbitals); interorbital space with granules; vertebral light line expanded in interocular and interscapular regions. Size range: males 44.5–57 mm, females 51.5–103 mm. This last specimen comes from Fray Bentos, Uruguay, and it is the largest specimen of the species that I have seen.

Distribution. This subspecies is found in Uruguay, probably over most of the country except the coastal portion from Nueva Palmira (upon the Uruguay River banks) to Montevideo; it occurs also in Fray Bentos (although on the Argentine side of the Uruguay River, in Gualeguaychú, *B. g. fernandezae* occurs) and in San Carlos (east of Montevideo). Some specimens from Montevideo are intermediate between this subspecies and *B. g. fernandezae;* specimens also with intermediate characters occur in Pôrto Alegre and Alto da Serra, in Brasil. In Argentina it is found in Buenos Aires Province from Chascomús and Saladillo to D'Orbigny (Partido de Coronel Suarez) and to the east it occurs in Mar del Plata upon the Atlantic coast.

Remarks. I have seen the type of *B. dorbignyi,* MNHN 4960. The catalogue data for the specimen mention the locality,

Montevideo, and collector, A. D'Orbigny (according to a letter from Dr. J. Guibé from the Muséum National d'Histoire Naturelle, Paris). For reasons previously explained (Gallardo, 1957: 340–342) I think that the true locality is Maldonado, Uruguay.

Literature citations referred to this subspecies. Hensel (1867: 141), Pôrto Alegre, Rio Grande do Sul, [material studied: ZMB 6803]; Cope (1885: 185), Rio Grande do Sul, probably São João do Monte Negro; Boulenger (1885a: 196, 1885b: 296, 1886: 442, 443), Rio Grande do Sul; Lutz (1934, pl. XXVII, figs. 1–1a), São Francisco de Paulo, Rio Grande do Sul, Brasil, Buenos Aires, Argentina. [The latter specimen is figured without a suborbital crest.] Cochran (1955: 25, pl. 3, figs. G–I), Alto da Serra, São Paulo, Brasil [material examined: USNM 102314, and the type (photograph, pl. 34, fig. F), also USNM 97188 from Buenos Aires Province, Argentina]. (Of the other specimens referred by Cochran to *B. g. dorbignyi,* USNM 65593–4, Malvin, Uruguay, and USNM 65578–80, Montevideo, Uruguay, are juvenile *Bufo arenarum.* Those still remaining have been cited above under *B. g. fernandezae.*) Klingelhöffer and Scherpner (1956: 160, fig. 127), photo of one specimen without a suborbital crest from southern Brasil. Gallardo (1957: 362, 363), Buenos Aires Province, Argentina (Libres des Sur, Chascomús, Rosas, Casalins, Tandil, Santo Domingo, Juancho, D'Orbigny, Cazón), San Carlos, Uruguay, and Pôrto Alegre, Brasil.

Material studied. **Uruguay.** Montevideo, MNHN 4960 type, MNHN 4959 (4 specimens). San Carlos, CNHM 9524–5. Near Fray Bentos, MCZ 1541 (2 specimens). **Argentina.** "Provincia de Buenos Aires," MZUM 94075, USNM 97188. Mar del Plata, Provincia de Buenos Aires, AMNH 33991–7, 34077–82. **Brasil.** *Rio Grande do Sul.* Pôrto Alegre, SM 21630, 30485, 21334–5, ZMB 6803 (4 specimens). *São Paulo.* Alto da Serra, USNM 102314.
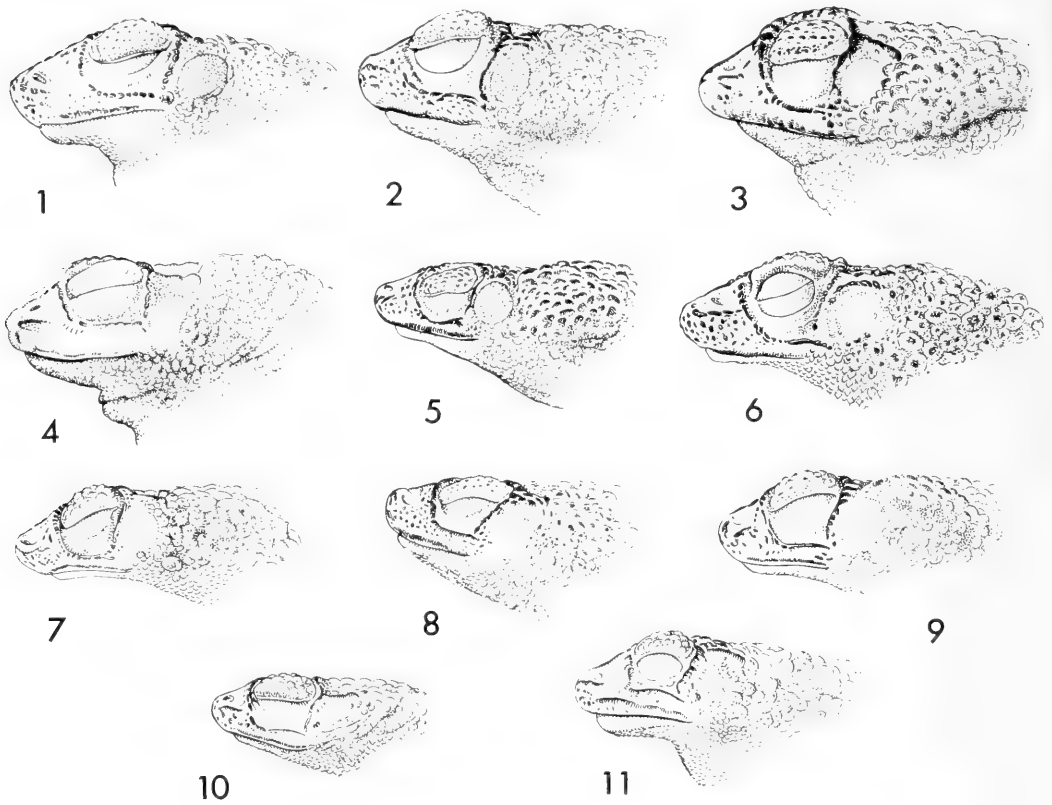
Fig. 2. Lateral views of heads of *Bufo granulosus* subspecies. 1. *B. g. granulosus*, USNM 97107. 2. *B. g. goeldii*, MZUM 64528. 3. *B. g. merianae*, AMNH 46531. 4. *B. g. minor*, MCZ 10089. 5. *B. g. beebei*, AMNH 55774. 6. *B. g. barbouri*, RNH 10867. 7. *B. g. mirandaribeiroi*, BMNH 1923.11.9.15. 8. *B. g. lutzi*, MZUM 108908. 9. *B. g. humboldti*, MCZ 24882. 10. *B. g. pygmaeus*, USNM 132357. 11. *B. g. azarai*, BMNH 1955.1.5.47.

DISCUSSION

When the different subspecies of *B. granulosus* are compared, two distinct types of heads are noticed: one, high, short and wide, and the other depressed, in general elongate, and narrow. To the first group belong: *B. g. granulosus*, *B. g. goeldii*, *B. g. merianae*, *B. g. minor*, *B. g. major*, *B. g. fernandezae*, *B. g. dorbignyi*, and to the second: *B. g. beebei*, *B. g. lutzi*, *B. g. mirandaribeiroi*, *B. g. barbouri*, *B. g. pygmaeus*, *B. g. azarai*.

The distribution of the subspecies with depressed heads is not continuous; instead, between *B. g. beebei* and the others of this series there are *B. g. merianae* and *B. g. goeldii* with high, short and wide heads.

The development of the crests varies among the subspecies. In some they are low and granular, in others they have rippled borders, and in some others they are considerably raised, as in *B. g. fernandezae*, *B. g. dorbignyi*, *B. g. merianae*, *B. g. azarai*. The degree of expansion of the maxillary crests varies considerably from one subspecies to another: in *B. g. granulosus* they are not expanded; in the subspecies of northern South America they are better marked, but achieve their greatest development in certain of the southern subspecies, i.e., *B. g. major*, *B. g. fernandezae*, *B. g. azarai* and especially in *B. g. dorbignyi*. The dorsal granules on the parotoids are rounded and flat in the subspecies of northeast and

southeast South America, but rather conical in *B. g. humboldti* from Colombia and Panama and very definitely conical in *B. g. major* of the Chacoan region.

It is not possible to arrange the subspecies of *B. granulosus* linearly, but they can be located on a branched scheme in which equivalent levels correspond to equivalent development in the cephalic crests. In such a diagram, which has only the object of providing a means of comparing the known subspecies, *B. g. granulosus* may be located at the base, as a subspecies with a short head, low and granular crests, and maxillary crests not expanded. This would lead, on one side, to *B. g. lutzi* (with somewhat elongate head, intermediate crests, maxillaries with a minimum of expansion), and, on the other side, to *B. g. goeldii* (with short and wide head, smooth and low crests, maxillaries somewhat expanded).

From *B. g. lutzi* would be derived *B. g. barbouri* (with intermediate head type, medium degree of prominence of the crests, borders scarcely rippled, maxillaries little expanded) and *B. g. mirandaribeiroi* (with head elongate and depressed, crests smooth and not elevated, maxillaries little expanded). From the latter would be derived: *B. g. beebei* (with elongate and depressed head, cephalic crests not very high and smooth, maxillaries barely expanded); *B. g. pygmaeus* (form of small size, head somewhat expanded and depressed, cephalic crests with smooth or somewhat rippled borders and relatively high, maxillaries somewhat expanded and suborbitals beyond postorbitals); *B. g. azarai* (head wide and depressed, with well developed cephalic crests, with smooth or somewhat rippled borders, maxillaries much expanded laterally, suborbitals also expanded and prolonged beyond postorbitals). These two latter subspecies are forms convergent to *B. g. fernandezae*, which has suborbitals expanded and prolonged beyond postorbitals.

From *B. g. goeldii* there could be derived *B. g. merianae* (with head short, laterally expanded and high, cephalic crests projecting and in general with rippled borders,

X B. g. dorbignyi

X B.g. fernandezae   X B.g. merianae

X B. g. azarai

X B. g. humboldti

X B. g. pygmaeus

X B. g. major

X B. g. minor

X B. g. barbouri

X B. g. goeldii

X B.g beebei

X B. g. mirandaribeiroi

X B. g. lutzi

X B. g. granulosus
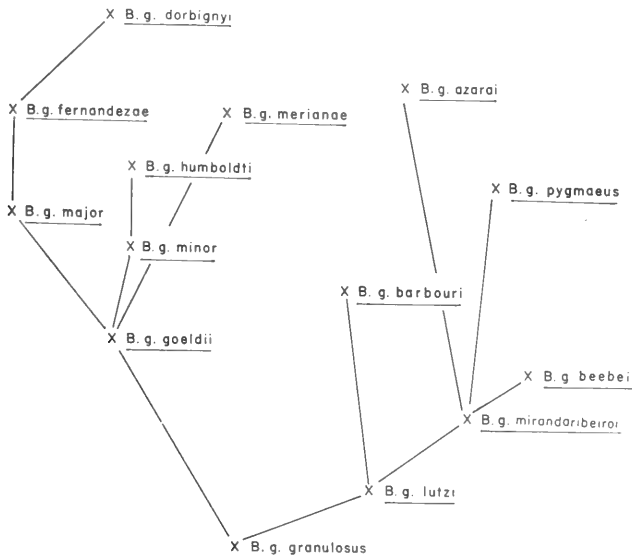
DENDROGRAM OF THE RELATIONSHIPS OF THE
SUBSPECIES OF Bufo granulosus Spix

maxillaries somewhat expanded and prolonged beyond postorbitals—convergent to *B. g. fernandezae*); *B. g. minor* (with short and high head, cephalic crests somewhat projecting and with generally rippled borders, maxillaries somewhat expanded) and from this *B. g. humboldti* (with head short, wide and high, projecting cephalic crests with rippled borders, maxillaries not very expanded, suborbitals expanded and somewhat prolonged beyond postorbitals); *B. g. major* (with head short, wide and high, cephalic crests with rippled or granular borders, somewhat projecting, maxillaries laterally expanded) and from this subspecies one could pass to *B. g. fernandezae* (with head short, wide and high, cephalic crests high, with smooth or little rippled borders, maxillaries somewhat expanded, suborbitals laterally expanded and prolonged beyond postorbitals). From *B. g. fernandezae* it is possible to pass to *B. g. dorbignyi* (with head short, wide and high, cephalic crests very high and with smooth or little rippled borders, maxillaries very wide). In this subspecies the supraorbital crests show maximum prominence as do the maxillaries, but the suborbitals and postorbitals are practically nonexistent.

ACKNOWLEDGMENTS

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TABLE 1

	granulosus	goeldii	merianae	minor	beebei	barbouri	miranda-ribeiroi
Head	Short, wide, high	Short, wide in buccal commissure, high	Short, wide in buccal commissure, high	Short, wide, high	Elongate, not wide, depressed	Moderately elongate, somewhat wide, depressed	Elongate, not wide, depressed
Loreal region	Nearly vertical	Nearly vertical	Nearly vertical	Somewhat concave	Sloping	Slightly sloping	Sloping, somewhat concave
Snout	Short	Very short	Short	Short	Elongate	Short, wide	Very broad, elongate
Rostrum	Slightly sloping	Nearly vertical	Nearly vertical	Nearly vertical	Sloping	Somewhat sloping	Sloping
Nostrils	Somewhat oblique	Oblique	Somewhat oblique	Somewhat oblique	Oblique	Oblique	Oblique
Cephalic crests	Low, granular or scalloped	Moderately developed, generally between smooth and rippled	Projecting, generally rippled	Somewhat projecting, generally rippled	Not very prominent, smooth or somewhat rippled	Somewhat elevated, generally lightly rippled	Not raised, smooth
Subnasal crests	Scarcely noticeable	Well defined, smooth	Noticeable	Projecting	Somewhat noticeable	Noticeable	Not projecting
Canthal crests	Granular	Smooth	Smooth	Smooth	Smooth	Smooth	Marked
Suborbitals, distance eye to eye	Very close; not prolonged	Little separated, somewhat expanded; not prolonged	Little separated; prolonged	Close; not prolonged	Close; prolonged by granules	Close; reaching a little beyond	Close; not prolonged
Preorbital crests	Well defined	Sloping	Sloping, with postorbitals and supra-orbitals making a rim around eye	Somewhat projecting	Projecting, a small flange in front of eye, sloping	Not very salient, sloping	Not raised, sloping
Postorbital crests	Well defined. Close to tympanum. Sloping	Close to tympanum. Sloping	Close to tympanum	Somewhat projecting. Close to tympanum	Close to tympanum. Sloping	Separated from tympanum	Not raised, near tympanum, sloping

TABLE 1. *Continued*

lutzi	humboldti	major	azarai	pygmaeus	fernandezae	dorbignyi
Moderately elongate, wide, depressed	Short, wide near eyes, high	Short, wide at buccal commissure, high	Short, wide, very depressed	Moderately elongate, wide at buccal commissure	Short, wide, high	Short, wide, high
Sloping, somewhat concave	Somewhat sloping	Sloping	Sloping, concave	Sloping	Somewhat sloping	Nearly vertical
Short	Short	Short	Very short	Short	Short	Very short
Somewhat sloping	Nearly vertical	Nearly vertical	Nearly vertical	Somewhat sloping	Nearly vertical	Nearly vertical
Oblique	Oblique	Oblique	Oblique	Oblique	Slightly oblique	Slightly oblique
Low, smooth or between granular and smooth	Salient, rippled	Somewhat raised, rippled or granular	Well developed, smooth or somewhat rippled	Relatively raised, smooth or somewhat rippled	High. Smooth or somewhat rippled	Very high. Smooth or somewhat rippled
Little marked	Scarcely visible	Quite visible, projecting	Visible	Visible	Visible	Quite visible
Not well marked	Smooth, a narrow intercanthal area	Smooth, a rather wide intercanthal area	Smooth	Smooth	Well developed	Very high
Close; not expanded or prolonged	Close; expanded, somewhat prolonged	Close; not expanded or prolonged	Well separated, small arch, expanded, prolonged	Close; not very expanded, prolonged	Rather distant. Expanded, prolonged	Not well marked
Slightly projecting	Well marked, somewhat sloping	Well marked, scarcely sloping	Marked	Somewhat sloping	Visible but not very prominent	Well defined
Slightly projecting, near tympanum, sloping	Well marked, near tympanum	Well marked, near tympanum, slightly sloping	Marked, somewhat separated from tympanum	Far from tympanum, sloping	Not very prominent. Far from tympanum	Very poorly marked

TABLE 2

	granulosus	*goeldii*	*merianae*	*minor*	*beebei*	*barbouri*	*miranda-ribeiroi*
Maxillary crests	Not expanded	Somewhat expanded	Somewhat expanded	Somewhat expanded	Scarcely expanded	Little expanded	Little expanded
Projecting laterally in dorsal view	Suborbitals	Maxillaries (slightly)	Suborbitals	Maxillaries (slightly)	Suborbitals	Suborbitals	Suborbitals
Maxillary ventral rim	Absent	Present	Present	Present	Narrow	Narrow	Narrow
Supra-orbital crests	Low	Not very high	Projecting, rippled, short oblique crests in parietal region	Only slightly projecting	Slightly raised, short divergent crests in parietal region	Slightly projecting, short divergent crests in parietal region	Slightly projecting. Short divergent crests in the parietal region
Inter-orbital space	Slightly concave, granular	Little concavity, granular, not very wide. Short crests at the canthal apex	Concave, granular. Short divergent crests at the canthal apex	Concave, granular. Short divergent crests at the canthal apex	Somewhat concave, granular. Short crests at the canthal apex	Slightly concave, granular. Short crests at the canthal apex	Somewhat concave, granular. Short crests at canthal apex
Parietal crests	Scarcely or not marked	Marked	Scarcely marked	Marked	Very short	Poorly marked	Slightly noticeable
Orbito-tympanic crests	Not well marked	Well marked	Marked	Marked	Well marked	Marked	Not expanded
Tympanum	Oblique	Oblique	Nearly vertical	Nearly vertical	Oblique	Slightly oblique	Gently sloping
Parotoids	Not prominent. Dorsal granules convex	Not prominent. Dorsal granules rounded	Large, not very prominent. Dorsal granules rounded	Prominent, lateral borders not well marked. Dorsal granules rounded, horny	Large. Dorsal granules large, rounded, flat	Not prominent. Dorsal granules small, conical	Not well marked. Dorsal granules rounded
Row of granules at tarsal inner edge	Present	Present	Present	Present	Present	Poorly marked	Hardly noticeable
Vertebral light line	Absent	Absent	Absent	Absent	Absent or just visible anteriorly	Absent	Present

TABLE 2.   *Continued*

lutzi	humboldti	major	azarai	pygmaeus	fernandezae	dorbignyi
Not expanded	Not very expanded	Laterally expanded	Very much expanded	Scarcely expanded	Somewhat expanded	Very expanded
Suborbitals	Suborbitals	Maxillaries	Maxillaries	Maxillaries	Suborbitals	Maxillaries
Narrow	Somewhat wide	Wide	Expanded	Somewhat expanded	Wide	Very expanded
Low. Without short divergent crests in the parietal region	Somewhat projecting	Somewhat projecting	Projecting. Short divergent crests in the parietal region	Somewhat raised	Developed. No upper eyelid	Very well developed. An upper eyelid
Somewhat concave, granular. Without divergent crests at canthal apex	Somewhat concave and wide. Short divergent crests at canthal apex	Concave, wide, granular. Short divergent crests at canthal apex	Concave, very wide, granular. Short divergent crests at canthal apex	Somewhat concave, granular	Somewhat concave, deep, granular	Very concave, deep. Without granules
Not well marked	Scarcely visible	Poorly marked	Marked	Marked	Well marked	Well marked
Not expanded	Expanded laterally	Not well marked	Thick border	Well marked	Well developed	Very high
Gently sloping	Gently sloping	Gently sloping	Gently sloping	Gently sloping	Nearly vertical	Not well marked. Nearly vertical
Rather prominent. Dorsal granules rounded	Subtriangular, not well marked. Dorsal granules conical or flat	Thin, with poorly marked borders. Dorsal granules conical, horny	Not prominent. Dorsal granules flat	Not prominent. Dorsal granules smooth	Subtriangular. Lower border not well marked. Dorsal granules flat	Subtriangular. Lower border not well marked. Dorsal granules flat
Poorly marked	Not well marked	Present	Hardly noticeable	Not well marked	Absent	Absent
Present	Absent	Absent	Generally absent	Generally present	Present	Present

Map 2.   Distribution of *Bufo granulosus* subspecies in northern South America.

Map 3. Distribution of *Bufo granulosus* subspecies in eastern Brasil.

SÃO JOÃO da BARRA

RESTINGA da MARAMBAIA

ALTO da SERRA

PÔRTO ALEGRE

CÁCERES

PÔRTO ESPERANCA

MIRANDA

MARACAJU

SAN JOSÉ de CHIQUITOS

BAHÍA NEGRA

PUERTO CASADO

PRIMA VERA

COLONIA MENNONITA

JUAREZ

ASUNCIÓN

SAN JOSÉ

NUEVA ITALIA

SANTO TOMÉ

LAS LOMITAS

RESISTENCIA

TATARENDA

EMBARCACIÓN

QUIMILI

YOFRE

MONTE CASEROS

BUENA VISTA

TOSTADO

VERA

PUERTO MARQUEZ

GUALEGUAYCHÚ

LEONES

LAZO

FRAY BENTOS

NUEVO PALMIRA

MALDONADO

DELTA

CARMELO

MONTE VIDEO

OTAMENDI

BUENOS AIRES

SANTO DOMINGO

TIGRE

LA PLATA

MERCEDES

PLATA

BELLA VISTA

CHASCOMÚS

CAZÓN

MAR del PLATA

ROSAS

TANDIL

D'ORBIGNY

B. g. dorbignyi

B. g. fernandezae

B. g. major

B. g. arenai

B. g. pygmaeus

Map 4. Distribution of *Bufo granulosus* subspecies in southern South America.

The Mesopelagic Fishes Collected During
Cruise 17 of the R/V Chain, with a
Method for Analyzing Faunal Transects

Richard H. Backus, Giles W. Mead, Richard L. Haedrich,
and Alfred W. Ebeling

THE MESOPELAGIC FISHES COLLECTED DURING CRUISE 17 OF THE R/V CHAIN, WITH A METHOD FOR ANALYZING FAUNAL TRANSECTS[1]

RICHARD H. BACKUS,[2] GILES W. MEAD,[2] RICHARD L. HAEDRICH,[2] AND ALFRED W. EBELING[3]

INTRODUCTION

Cruise 17 of the R/V CHAIN of the Woods Hole Oceanographic Institution was devoted mainly to hydrographic, bathymetric, and geochemical studies in the Atlantic Ocean in the neighborhood of the Romanche Trench, a depression lying on the equator at about 17° West. On the homeward leg of this cruise (April 20–May 15, 1961), 14 collections (800–813) were made by the senior author with a 10-foot Isaacs-Kidd midwater trawl (IKMT) (Fig. 1). Earlier in the cruise, four successful collections (4, 5, 6, and 9) had been made by Mr. Herbert Curl, Jr., with a three-foot IKMT. The fishes taken have been identified, and provide data from which we derive a method for the analysis of such faunal transects. The application of this method, together with ancillary physical observations, permits some tentative remarks on faunal boundaries in the southern North Atlantic Ocean.

Collection data, together with the numbers of species and specimens taken (exclusive of larvae), are given in Table 1. The tows were made at about 3½ knots, and all but one took place at night. Their

depths were computed from measurements of wire angle and amount of wire out and are considered to be accurate to about ±5 per cent. This procedure is justified by the findings of Backus and Hersey (1956) who compared the results of such computations with echo-sounder measurements of the depth of an IKMT made from a following ship. Comparisons of computed depths with measurements made using a time-depth recorder (Benthos Company Depth Recorder) were made on a cruise in early 1963. These again justify the use of triangulation for determining the depth of the IKMT, at least with towing warps a few hundred meters long and towing speeds of about 5 knots or less.

As no closing device was used with the net during CHAIN Cruise 17, we cannot be certain that any specimen came from the depth given for the net. However, the time at depth was made long with respect to the time consumed in setting and hauling the net.

Fishing depths were chosen which promised to yield large amounts of material. Choices were based on inspection of the echo-sounder record (Edo Corporation UQN-1b with the Precision Graphic Recorder; operating frequency, 12 kcps) for the deeper hauls (230–495 m) and the echo-sounder record and a bathythermogram for the shallower hauls (42–90 m). For the deeper hauls the depth of a pronounced sound-scattering maximum was chosen. For
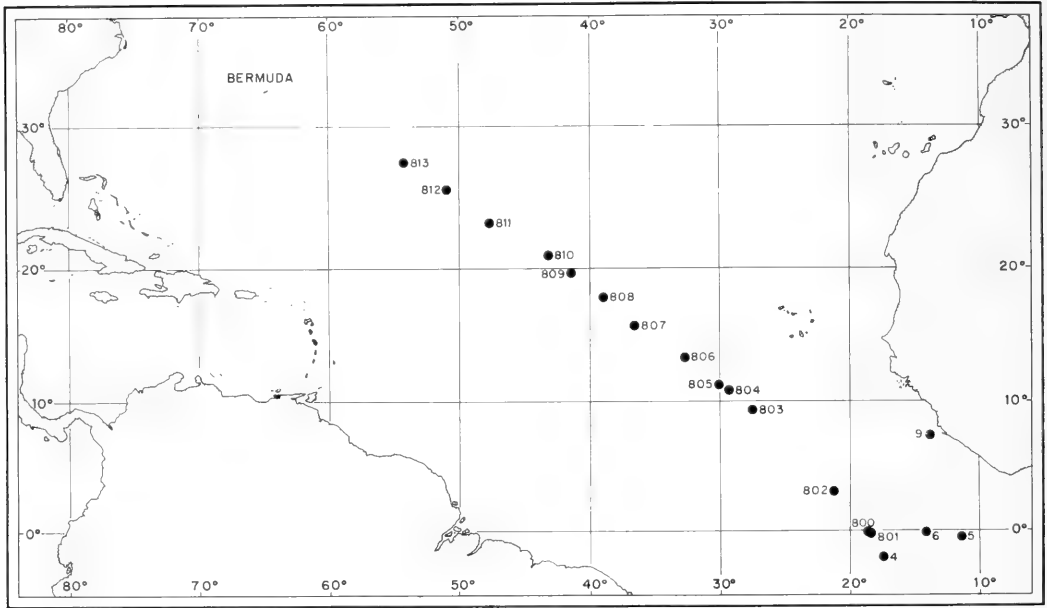
Fig. 1.   Location of collections.

the shallower hauls some critical point on the temperature-depth curve that lay within a zone of intense sound-scattering was chosen. The bottom of an isothermal layer, the bottom of a thermocline, and the level of a pronounced temperature inversion all appear to be places where animals tend to concentrate.

It is traditional in oceanography to make the samples comparable in depth when sampling over a long section. The only property of the environment held approximately constant by such a choice is pressure. This property seems of relatively little importance in the lives of pelagic animals, at least when compared with temperature, transparency and probably many other properties. In measuring such a factor as temperature, a successful observation is assured, given a working instrument. Often in collecting pelagic fishes, however, "no catch" results from a haul at an arbitrarily chosen depth. While this may be an interesting ecological observation, it is generally considered unsatisfactory when the purpose is zoogeographical.

The cruise was conducted under Contracts 2196 and 3351 between the Office of Naval Research and the Woods Hole Oceanographic Institution. Other parts of the work have been supported by National Science Foundation Grants G-9579 and GB-543 to the Woods Hole Oceanographic Institution and G-15887 to Harvard University. We are greatly indebted to these organizations for their help, and to Vaughan T. Bowen and W. G. Metcalf, the organizers of the cruise. Metcalf provided the bathythermograph data used. Charles Karnella sorted many of the collections. Robert H. Gibbs, Jr., U. S. National Museum, identified the stomiatoid fishes, except for the sternoptychids and the gonostomatids. The last were identified by the late Marion Grey, Chicago Natural History Museum. Daniel M. Cohen, U. S. Bureau of Commerical Fisheries, identified most of the anacanthine fishes. Loren P. Woods, Chicago Natural History Museum, identified the specimens of *Diretmus*. George S. Myers, Stanford University, identified the *Neocyttus helgae*. N. B. Marshall identified

n.STREKALOVSKY
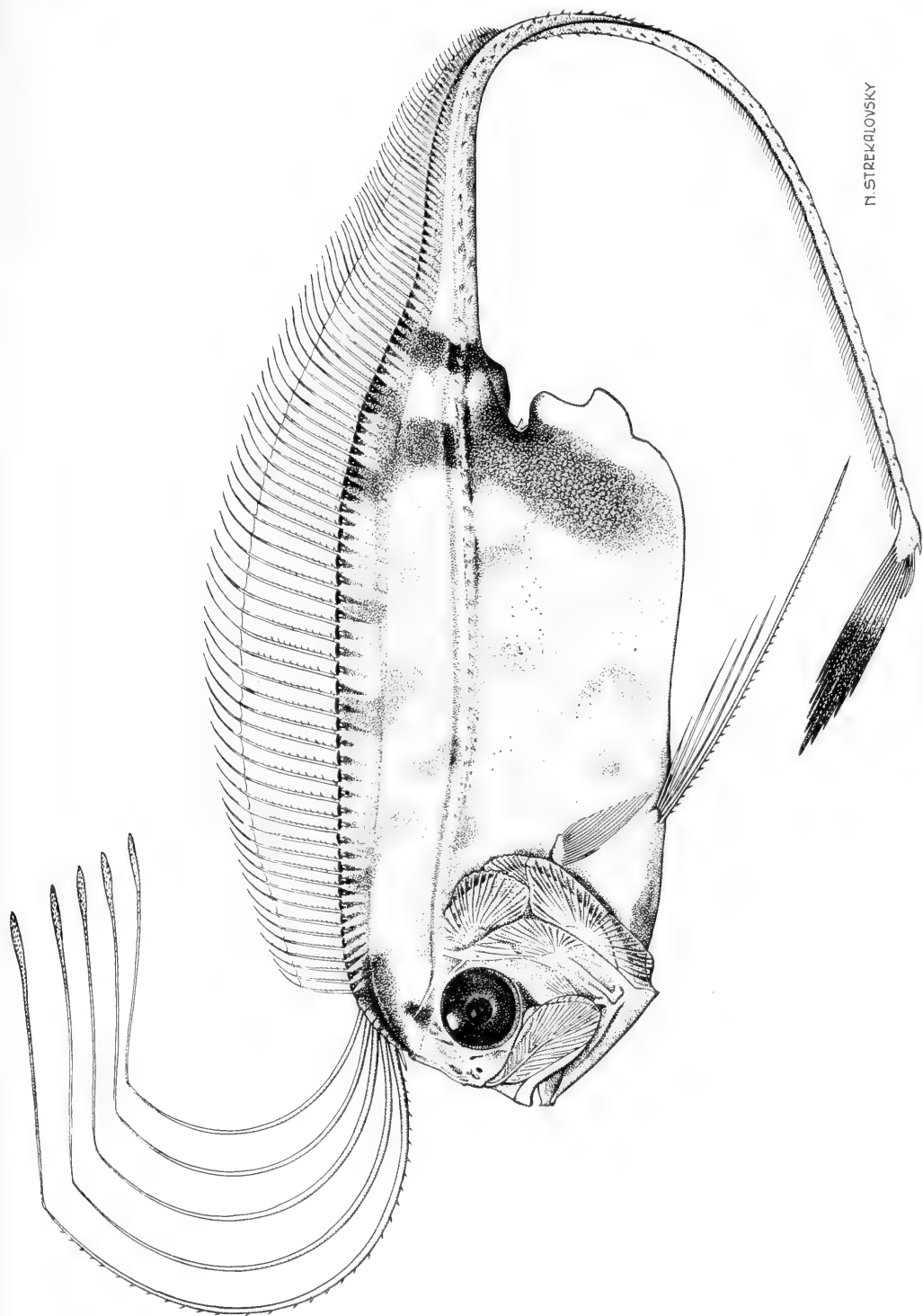
Fig. 2. *Zu cristatus* (Bonelli, 1820). 120 mm S. L.

TABLE 1.   COLLECTION DATA ASSOCIATED WITH MIDWATER TRAWL HAULS, CRUISE 17, R/V CHAIN

COLLEC-TION	POSITION	DATE (1961)	TIME (LOCAL)	DEPTH (m)	TEMPERATURE (°C)			No. OF SPECIES	No. OF SPECI-MENS
					Surf.	at net[1]	200 m[5]		
4	02°10'S., 17°25'W.	2 April	0010–0225	–[1]	29.0	–	12+	19	30
5	00°35'S., 11°30'W.	3 April	2145–2230	–	28.5	–	12+	16	32
6	00°05'S., 14°15'W.	4 April	1955–2200	–	29.0	–	12+	14	45
9	07°15'N., 14°00'W.	20 April	2140–2335	–[2]	30.0	–	14+	26	43
800[3]	00°12'S., 18°40'W.	24–25 April	2320–0240	85	29.5	18.5	13+	17	47
801	00°15'S., 18°40'W.	26 April	0250–0605	85	29.5	18.5	13+	34	82
802	03°00'N., 21°15'W.	27–28 April	2020–0020	275	29.0	10.5	13+	32	69
803	09°27'N., 27°45'W.	1 May	0340–0725	275	25.0	10.0	11+	24	140
804	10°55'N., 29°30'W.	1–2 May	2200–0110	42	25.0	22.0	11+	24	947
805	11°17'N., 30°00'W.	2–3 May	2015–0045	230	24.5	11.5	11+	35	101
806	13°30'N., 32°55'W.	3–4 May	2030–0040	70	23.5	19.0	11+	31	629
807	16°00'N., 36°20'W.	4–5 May	2125–0250	430	23.5	10.0	15+	13	30
808	18°00'N., 39°00'W.	5–6 May	2010–0115	290	24.0	13.0	16+	15	30
809	19°40'N., 41°20'W.	6 May	1930–2235	70	24.0	23.0	18+	16	62
810	20°55'N., 43°15'W.	7 May	0920–1355	495	24.5	11.0	19+	7	154
811	23°15'N., 47°05'W.	8 May	2035–2340	90	25.0	23.0	19+	15	66
812	25°40'N., 50°50'W.	9–10 May	2115–0040	70	24.0	21.5	18+	18	104
813	27°30'N., 54°05'W.	10–11 May	2110–0220	53	23.5	23.0	18+	13	97

[1] 0–1800 m of wire out.
[2] 0–400 m of wire out.
[3] Bridle broke part way through tow closing the net.
[4] Numbers in roman type are from bathythermograph observations made at time of collection; numbers in italics are from Fuglister (1960).
[5] From E. Schroeder (1963).

the *Sphagemacrurus*. Basil Nafpaktitis aided greatly in the identification of fishes in the genus *Diaphus*. Otherwise the determinations are those of the authors. The specimens have been deposited in the Museum of Comparative Zoology, Harvard University. We are especially indebted to Gibbs and Mrs. Grey, who not only identified large amounts of material, but also read and improved the manuscript. We are grateful as well to V. T. Bowen, N. B. Marshall, G. G. Simpson, D. W. Bourne and L. V. Worthington for their criticism. James Rohlf advised us in statistical matters. The drawings of fishes were done by N. Strekalovsky.

LIST OF SPECIES

Following the species name are the station numbers at which the species was taken, and, in parentheses, the number of specimens and range of standard lengths. In some cases, determinations were not positive, and we have introduced the use of opposed question marks (following the Spanish

custom) for setting off that part of the scientific name held in doubt.
Selachii (Squaloidea)
    Dalatiidae
        Isistius brasiliensis (Quoy and Gaimard, 1824). 4 (1, 350 mm t. l.); 5 (1, 425 mm t. l.); 801 (1, 320 mm t. l.); 802 (1, 265 mm t. l.); 805 (1, 265 mm t. l. This material does not include a new western Atlantic species, *I. plutodus* Garrick and Springer, 1964.
Isospondyli
    Clupeoidea
        Alepocephalidae
            Holtbyrnia sp. 802 (1, 43.2 mm)
    Argentinoidea
        Bathylagidae
            Bathylagus ¿ argyrogaster Norman, 1930? 9 (2, 29.0 & 62.0 mm); 801 (2, 30.8 & 79.0 mm)
        Opisthoproctidae
            Opisthoproctus grimaldii Zugmayer, 1911. 803 (2, 55.0 & 55.5 mm); 805 (1, 20.9 mm)
            Opisthoproctus soleatus Vaillant, 1888. 4 (1, 71.0 mm)
    Stomiatoidea
        Sternoptychidae
            Argyropelecus aculeatus Cuvier and Val-

enciennes, 1849. 805 (14, 9.9–15.6 mm); 808 (2, 11.2 & 53.5 mm); 810 (1, 16.6 mm)

Argyropelecus affinis Garman, 1899. 4 (3, 17.8–52.5 mm); 6 (18, 53–55 mm); 802 (1, 15.0 mm); 807 (5, 13.4–24.0 mm)

Argyropelecus gigas Norman, 1930. 6 (1, 61.8 mm)

Argyropelecus hemigymnus Cocco, 1829. 4 (1, 23.5 mm); 802 (1, *ca.* 18.0 mm); 807 (1, 20.5 mm)

Argyropelecus lychnus lychnus Garman, 1899. 5 (4, 15.3–51.5 mm); 6 (3, 12.6–29.6 mm); 9 (1, 20.4 mm); 802 (1, 10.8 mm); 803 (3, 10.7–30.8 mm); 805 (3, ?–51.3 mm); 807 (3, 11.0–11.5 mm)

Polyipnus polli Schultz, 1961. 5 (1, 18.7 mm)

Sternoptyx diaphana Hermann, 1781. 802 (6, 16.3–29.0 mm); 805 (1, 15.5 mm)

Gonostomatidae

Bonapartia pedaliota Goode and Bean, 1896. 4 (2, 35.5 & 62.0 mm); 5 (4, 38.5–57.0 mm); 6 (7, 46.5–66.0 mm); 9 (1, *ca.* 25 mm); 802 (9, 38.5–44.0 mm); 803 (32, 30.0–50.5 mm); 805 (2, 50.0 & 52.5 mm)

Cyclothone sp. 4 (5, *ca.* 14–28 mm); 802 (1, 26.5 mm); 803 (5, *ca.* 15–20 mm); 805 (1, 24.5 mm); 808 (1, 21.5 mm); 810 (145, less than 20.5 mm); 811 (5, small and damaged)

Diplophos taenia Günther, 1873. 805 (3, *ca.* 28 mm); 806 (2, 69.5 & 106.0 mm)

Gonostoma atlanticum Norman, 1930. 802 (6, 22.0–51.0 mm); 803 (18, 38.5–55.0 mm); 805 (4, 38.5–49.0 mm); 807 (3, 44.0–59.5 mm)

Gonostoma denudatum Rafinesque, 1810. 802 (1, 90.0 mm)

Gonostoma elongatum Günther, 1878. 805 (2, 153.0 & 187.0 mm)

Gonostoma sp. 800 (1, *ca.* 33.5 mm); 805 (1, 22.5 mm); 806 (18, 15.0–26.0 mm)

Ichthyococcus ovatus (Cocco, 1840). 802 (3, 34.5–43.5 mm); 803 (6, 18.5–41.5 mm); 805 (1, 22.5 mm); 806 (4, 22.0–35.5 mm); 810 (1, 21.5 mm)

Margrethia obtusirostra Jespersen and Tåning, 1919. 808 (1, 37.0 mm)

Maurolicus muelleri (Gmelin, 1789). 804 (3, 14.5–26.5 mm); 806 (2, 14.5 & 15.0 mm)

Pollichthys mauli (Poll, 1953). 9 (2, 39.0 & 47.0 mm); 813 (5, 37.0–40.5 mm)

Valenciennellus tripunctulatus (Esmark, 1870). 6 (1, 30.5 mm); 802 (4, *ca.* 28.0–30.0 mm); 803 (2, 20.0 & 28.0 mm); 805 (1, 25.5 mm); 807 (9, 23.0–30.5 mm); 808 (4, 13.0–18.0 mm); 810 (3, 21.0–22.5 mm)

Vinciguerria nimbaria (Jordan and Williams, 1895). 6 (5, 26.0–*ca.* 36.0 mm); 9 (1, 35.0 mm); 800 (16, *ca.* 24.0–29.0 mm); 801 (8, 27.0–33.0 mm); 802 (1, 28.0 mm); 803 (31, 15.5–36.5 mm); 804 (159, 15.0–40.0 mm); 806 (100, 15.5–36.0 mm); 809 (7, 19.5–41.5 mm); 811 (1, 40.5 mm)

Vinciguerria sp. 9 (1, *ca.* 13 mm); 804 (245 young, 13.5–18.5 mm); 805 (1, *ca.* 28 mm); 806 (28, 14.0–18.0 mm); 810 (2, 14.5 & 15.5 mm)

Astronesthidae

Astronesthes caulophorus Regan and Trewavas, 1929. 9 (1, 54.4 mm)

Astronesthes cyaneus (Brauer, 1902). 9 (1, 27.3 mm)

Astronesthes richardsoni Poey, 1852. 5 (1, 94.5 mm); 9 (1, 27.0 mm); 805 (1, 93.5 mm); 806 (6, 30.7–52.0 mm)

Heterophotus ophistoma Regan and Trewavas, 1929. 6 (1, 212.9 mm); 802 (1, 154.4 mm)

Chauliodontidae

Chauliodus danae Regan and Trewavas, 1929. 807 (2, 83.5 & 93.2 mm); 808 (4, 72.1–93.1 mm); 811 (1, 86.4 mm)

Chauliodus schmidti Ege, 1948. 804 (2, 32.1–37.5 mm); 805 (1, 135.4 mm)

Chauliodus sloani Bloch and Schneider, 1801. 802 (1, 156.7 mm)

Idiacanthidae

Idiacanthus fasciola Peters, 1885. 809 (1, *ca.* 270 mm); 813 (5, 54.1–96.4 mm)

Stomiatidae

Stomias affinis Günther, 1885. 802 (3, 85.9–93.5 mm); 804 (4, 25.4–36.5 mm); 806 (1, 43.4 mm)

Melanostomiatidae

Bathophilus brevis Regan and Trewavas, 1930. 804 (2, 17.1 & 35.6 mm)

Bathophilus nigerrimus Giglioli, 1884. 6 (1, 83.2 mm)

Bathophilus pawneei Parr, 1927. 801 (1, 58.5 mm); 809 (1, 25.7 mm)

Echiostoma barbatum Lowe, 1843. 811 (1, 158.1 mm); 812 (1, 113.5 mm)

Eustomias melanostigma Regan and Trewavas, 1930. 9 (1, 85.4 mm)

Eustomias obscurus Vaillant, 1888. 804 (1, 68.6 mm); 812 (1, 77.9 mm)

Leptostomias (cf. *gracilis* Regan and Trewavas, 1929). 805 (1, 147.6 mm); 806 (1, 72.2 mm)

Melanostomias biseriatus Regan and Trewavas, 1930. 9 (1, 181.7 mm)

Melanostomias tentaculatus (Regan and Trewavas, 1930). 811 (1, 53.5 mm)

Photonectes parvimanus Regan and Trewavas, 1930. 812 (1, 28.2 mm)

Malacosteidae

Aristostomias ¿*tittmanni* Welsh, 1923? 801 (1, 102.7 mm); 802 (1, 130.5 mm)

Photostomias guernei Collett, 1889. 9 (1, 35.7 mm); 812 (2, 29.3 & 40.5 mm)

Iniomi

Myctophidae

Benthosema suborbitale (Gilbert, 1913). 801 (1, 11 mm); 804 (5, 13–26 mm); 806 (122, 10–31 mm); 808 (4, 10–26 mm); 809 (4, 21–24 mm); 811 (1, 28 mm); 812 (3, 24–26 mm)

Ceratoscopelus townsendi (Eigenmann & Eigenmann, 1889). 4 (2, 21 & 21 mm); 5 (1, 54 mm); 9 (1, 20 mm); 800 (1, 70 mm); 801 (1, 25 mm); 804 (27, 22–50 mm); 806 (25, 22–59 mm); 808 (1, 62 mm); 809 (5, 17–62 mm); 811 (5, 20–62 mm); 812 (14, 17–62 mm); 813 (12, 18–55 mm)

Diaphus brachycephalus Tåning, 1928. 800 (2, 40 & 41 mm); 801 (13, 21–42 mm); 808 (1, 33 mm)

Diaphus dofleini (Zugmayer, 1911). 4 (1, 45 mm); 5 (1, *ca.* 50 mm); 801 (1, 34 mm); 803 (3, 25–46 mm); 804 (1, 22 mm)

Diaphus dumerili (Bleeker, 1856). 801 (1, 58 mm)

Diaphus effulgens (Goode and Bean, 1896). 812 (12, 18–31 mm)

Diaphus elucens (Brauer, 1904). 806 (8, 38–55 mm)

Diaphus fragilis Tåning, 1928. 800 (1, 30 mm); 801 (1, 40 mm); 806 (53, 35–76 mm); 809 (4, 49–50 mm)

Diaphus gemellari (Cocco, 1838). 806 (5, 27–31 mm); 808 (5, 37–57 mm); 809 (1, 29 mm); 810 (1, 38 mm); 811 (3, 27–31 mm); 812 (1, 14 mm)

Diaphus ¿*intermedius* Borodin, 1930? 807 (1, 65 mm). This specimen closely resembles Borodin's type of *intermedius*, but the status of this species is unresolved. Perhaps it is a synonym of *D. rafinesquei.*

Diaphus lucidus (Goode and Bean, 1896). 5 (1, 70 mm); 800 (1, 51 mm); 801 (1, 51 mm); 802 (1, 59 mm); 805 (1, 56 mm)

Diaphus luetkeni (Brauer, 1904). 4 (1, 50 mm); 9 (2, 33 & 40 mm); 800 (2, 28 & 35 mm); 801 (1, 30 mm); 802 (11, 44–49 mm); 803 (3, 31–53 mm); 804 (5, 17–28 mm); 805 (2, 26 & 48 mm); 806 (10, 10–26 mm); 807 (1, 36 mm)

Diaphus mollis Tåning, 1928. 800 (1, 39 mm); 804 (1, 19 mm); 806 (12, 19–40 mm); 809 (2, 15 & 26 mm); 810 (1, 34 mm); 812 (7, 20–42 mm); 813 (5, 15–29 mm)

Diaphus problematicus Parr, 1928. 800 (1, 60 mm); 808 (1, 56 mm); 811 (1, 65 mm)

Diaphus splendidus (Brauer, 1904). 811 (6, 41–47 mm)

Diaphus termophilus Tåning, 1928. 808 (1, 35 mm)

Diaphus sp. A. 4 (2, 25 & 26 mm); 5 (2, 24 & 26 mm); 9 (3, *ca.* 15 mm); 801 (1, 21 mm); 803 (3, 18–26 mm); 804 (94, 11–26 mm). The Dn and Vn appear to form a single large antorbital organ. The first and last AOa are elevated, the first markedly so. In 25 specimens counted, the AO were $6 + 5$ (11 specimens), $6 + 4$ (10), $5 + 5$ (2), $7 + 4$ (1), and $5 + 6$ (1). Related to *D. rafinesquei.*

Diaphus sp. B. 801 (1, 50 mm). Dn roughly circular and mainly directed forward. Vn separate from Dn and larger, extending rearwards to level of anterior edge of lens. AO $6 + 4$. AOa_1 not quite above line conecting tops of AOa_2 and AOa_3. AOa_{4-6} make ascending series. Photophores very large, the AOp being scarcely separated.

Diogenichthys atlanticus (Tåning, 1928). 801 (1, 13 mm); 803 (1, 44 mm); 804 (87, 13–22 mm); 806 (65, 13–21 mm)

Electrona rissoi (Cocco, 1829). 6 (1, *ca.* 40 mm); 803 (1, 39 mm)

Hygophum macrochir (Günther, 1864). 5 (5, 29–71 ? mm); 9 (3, 11–41 mm); 801 (13, 17–39 mm); 803 (1, 28 mm); 804 (69, 12–49 mm); 805 (1, 46 mm); 806 (3, 16–18 mm); 809 (2, 25 & 44 mm)

Hygophum reinhardti (Lütken, 1892). 803 (1, 42 mm); 804 (1, 41 mm); 806 (1, 43 mm); 808 (1, 40 mm); 812 (2, 17 & 19 mm)

Lampadena nitida Tåning, 1928. 801 (1, 50 mm)

Lampanyctus alatus Goode and Bean, 1896. 9 (1, 20 mm); 800 (4, 40–44 mm); 801 (4, 40–44 mm); 802 (1, 35 mm); 806 (4, 18–36 mm)

Lampanyctus crocodilus (Risso, 1810). 806 (20, 22–59 mm)

Lampanyctus cuprarius Tåning, 1928. 812 (9, 27–35 mm); 813 (2, 27 & 29 mm)

Lampanyctus ¿*lineatus* Tåning, 1928? 805 (5, 39–116 mm)

Lampanyctus macropterus (Brauer, 1904). 800 (3, 67–82 mm); 801 (4, 66–79 mm); 802 (3, 52–69 mm); 809 (9, 34–47 mm)

Lampanyctus photonotus Parr, 1928. 802 (1, 55 mm); 809 (13, 22–56 mm); 811 (25, 21–58 mm); 812 (9, 18–43 mm); 813 (21, 19–57 mm)

Lampanyctus ¿*tenuiformes* (Brauer, 1906)? 813 (3, 18–19 mm)

Lepidophanes gaussi (Brauer, 1906). 809 (2, 26 & 35 mm); 811 (12, 30–36 mm);

812 (5, 25–35 mm); 813 (10, 17–32 mm)
Lepidophanes guentheri (Goode and Bean, 1896). 4 (1, 30 mm); 5 (6, 20–47? mm); 6 (3, 45–60 mm); 9 (1, 24 mm); 801 (5, 37–47 mm); 802 (2, 39–42 mm); 803 (9, 29–75 mm); 804 (71, 15–57 mm); 806 (4, 45–50 mm); 808 (2, 36 & 61 mm); 811 (1, 66 mm); 813 (2, 45 & 56 mm)
Lepidophanes pyrsobolus (Alcock, 1890). 5 (1, 50 mm); 806 (1, 23 mm); 807 (1, 68 mm); 808 (1, 28 mm); 809 (3, 19–22 mm); 811 (2, 17 & 30 mm); 812 (7, 12–20 mm); 813 (8, 12–22 mm)
¿Loweina ? sp. 9 (1, 23 mm)
Myctophum affine (Lütken, 1892). 800 (3, 34–46 mm)
Myctophum asperum Richardson, 1844. 5 (1, 33 mm); 801 (1, 53 mm); 804 (14, 24–59 mm)
Myctophum ¿asperum Richardson, 1844? 6 (1, 16 mm); 9 (2, 16 & 25 mm)
Myctophum nitidulum Garman, 1899. 800 (2, 49 & 49 mm); 802 (1, 72 mm)
Myctophum sp. 801 (1, 16 mm)
Notolychnus valdiviae (Brauer, 1904). 9 (5, *ca.* 20 mm); 803 (5, 18–20 mm); 804 (39, 12–22 mm); 806 (94, 11–22 mm); 809 (6, 16–19 mm); 812 (27, 14–20 mm); 813 (21, 15–21 mm)
Notoscopelus caudispinosus (Johnson, 1863). 4 (1, *ca.* 55 mm); 811 (1, 86 mm)
Notoscopelus resplendens (Richardson, 1844). 4 (1, 69 mm); 801 (1, 64 mm); 803 (1, broken); 804 (101, 22–83 mm); 805 (1, 72 mm); 806 (31, 26–71 mm)
Symbolophorus rufinus (Tåning, 1928). 806 (1, 46 mm)
Paralepididae
Lestidiops affinis (Ege, 1930). 802 (1, 97.5 mm)
Paralepis atlantica Krøyer, 1891. 801 (1, 97.5 mm)
Scopelarchidae
Neoscopelarchoides dubius Marshall, 1955. 807 (1, 119.0 mm)
Neoscopelarchoides sp. A. 801 (1, 41.5 mm)
Scopelarchus guentheri Alcock, 1896. 805 (1, 76.1 mm)
Scopelarchus sp. A. 801 (1, 43.0 mm); 803 (1, 37.6 mm)
Evermannellidae
Evermannella balbo (Risso, 1820). 804 (7, 7.4–16.5 mm)
Evermannella indica Brauer, 1906. 805 (2, 58.8 & 65.8 mm); 812 (1, 23.7 mm); 813 (2, 22.5 & 27.0 mm)
Evermannella sp. A. 6 (1, 37.8 mm); 800 (1, 27.0 mm); 801 (6, 26.3–29.0 mm). These specimens probably represent an un-

described form related to *E. sicaria* Rofen, 1960, but have fewer anal rays (29–32 cf. 35 or 36) and, as postlarvae, lack discrete rows of spots on the sides of the body. As all eight specimens are postlarval, the description and christening of this form are deferred.
Allotriognathi
Trachypteridae
Zu cristatus (Bonelli, 1820). 804 (1, 35.3 mm); 809 (1, 120.0 mm, Figure 2)
Stylephoridae
Stylephorus chordatus Shaw, 1791. 807 (1, 130.0 mm). The specimen has been forwarded, for dissection, to Dr. Werner Meinel, Zoologisches Institut der Justus Liebig—Universität, Giessen.
Apodes
Derichthyidae
Derichthys serpentinus Gill, 1887. 807 (1, 219.0 mm)
Nemichthyidae
Nemichthys scolopaceus Richardson, 1848. 4 (1, 530+ mm); 6 (1, 365.0 mm); 802 (1, 365.0 mm); 805 (1, 545.0 mm); 807 (1, 305.0 mm)
Nessorhamphidae
Nessorhamphus ingolfianus Schmidt, 1930. 802 (1, 82+ mm)
Anacanthini
Gadoidea
Moridae
Melanonus zugmayeri Norman, 1930. 4 (2, 76.4 & 206.0 mm); 9 (1, 82.7 mm); 802 (1, 81.5 mm); 805 (3, 94.1–114.8 mm)
Bregmacerotidae
Bregmaceros atlanticus Goode and Bean, 1896. 4 (2, 39.8 & 40.0 mm); 801 (1, 35.0 mm); 812 (1, 20.0 mm)
Macrouroidea
Macrouridae
¿Sphagemacrurus? sp. 803 (1, 153.0 mm, Figure 3).
Xenoberyces
Melamphaidae
Melamphaes eulepis Ebeling, 1962. 9 (1, 29.4 mm); 803 (1, 19.3 mm)
Melamphaes longivelis Parr, 1933. 803 (1 young)
Melamphaes polylepis Ebeling, 1962. 9 (2, 18.5 & 19 mm)
Melamphaes simus Ebeling, 1962. 9 (5, 16–21 mm); 805 (2, 24.5 & 24.0 mm)
Melamphaes typhlops (Lowe, 1843). 805 (1, *ca.* 42.0 mm)
Poromitra megalops (Lütken, 1877). 4 (1, 32.2 mm); 5 (1, 20.9 mm)
Scopelogadus beanii (Günther, 1887). 5(1, 54.9 mm)
Scopelogadus mizolepis mizolepis (Günther,

1878). 4 (1, 67.2 mm); 5 (1, 30.3 mm); 800 (1, 23.0 mm); 801 (1, 30.0 mm); 802 (1, 54.5 mm); 803 (2, 62.0 & 79.0 mm); 805 (16, 39.0–68.5 mm); 808 (1, 57.8 mm)

Berycomorphi
  Diretmidae
    Diretmus argenteus Johnson, 1863. 4 (1, 22.0 mm); 801 (3, 12.0–16.0 mm); 803 (7, 14.5–26.0 mm); 805 (19, 16.1–28.0 mm)
    Diretmus sp. A. 9 (1, 60.0 mm); 800 (1, 14.0 mm)

Zeomorphi
  Zeidae
    Neocyttus helgae (Holt and Byrne, 1908)? 805 (1, 72.5 mm, Figure 4).

Percomorphi
  Percoidea
    Bramidae
      Brama dussumieri Cuvier and Valenciennes, 1831. 6 (1, 18.5 mm); 804 (3, 27.8–80.7 mm); 806 (1, 33.1 mm)
      Taractes asper Lowe, 1843. 806 (1, 15.6 mm)
    Cheilodipteridae
      Bathysphyraenops simplex Parr, 1933. 800 (6, 12.5–18.2 mm); 802 (1, 59.6 mm); 806 (1, 33.1 mm)
    Chiasmodontidae
      Chiasmodon niger Johnson, 1863. 801 (1, 30.2 mm)
      Chiasmodon sp. A. 805 (3, 40.3–49.8 mm)
      Pseudoscopelus altipinnis Parr, 1933. 802 (1, 90.2 mm); 805 (1, 118.0 mm)
      Pseudoscopelus sp. A. 801 (1, 33.8 mm). The specimen has a higher number of dorsal and anal fin rays and a more blunt snout, but is otherwise similar to *Pseudoscopelus stellatus* Beebe, 1932.
    Caristiidae
      Caristius japonicus Gill and Smith, 1905. 805 (1, 21.3 mm)
  Scombroidea
    Gempylidae
      Gempylus serpens Cuvier and Valenciennes, 1831. 806 (1, 50 mm); 809 (1, *ca.* 35 mm)
      Nealotus tripes Johnson, 1865. 805 (1, 40 mm)
    Trichiuridae
      Diplospinus multistriatus Maul, 1948. 806 (4, 58–85 mm); 812 (1, *ca.* 24 mm)
  Stromateoidea
    Nomeidae
      Psenes maculatus Lütken, 1800. 804 (5, 13.5–17.5 mm)
Plectognathi
  Molidae
    Mola mola (Linnaeus, 1758). 813 (1, 6.4 mm)

The list comprises 2,708 specimens in 369 species lots. One-hundred-thirty species, 73 genera, 35 families and 11 orders are represented. Each of 54 species was collected at a single station only; 41 of these were represented by a single specimen. Each of 28 species was collected at two stations, 12 at three, 9 at four, 10 at five, 3 at six, 7 at seven, 3 at eight, 0 at nine, 2 at ten, 0 at eleven, and 2 at twelve. No species was collected at more than 12 of the 18 stations. The myctophid fishes *Ceratoscopelus townsendi* (12 lots, 95 specimens) and *Lepidophanes guentheri* (12 lots, 107 specimens) were the most widespread. The most abundant species was *Vinciguerria nimbaria* (329 specimens, 10 lots).

DISCUSSION

Several recent contributions to pelagic zoogeography have stressed the relationship between the distribution of animal species and oceanic water masses, defined principally by temperature-salinity relationships (e.g., Pickford, 1946; Haffner, 1952; Bieri, 1959; McGowan, 1960; Brinton, 1962; Ebeling, 1962; Fager and McGowan, 1963; and Ebeling and Weed, 1963). While a species may be confined to a part of a water mass, be distributed throughout a water mass, or be found in two or more water masses, the conformance of the boundaries, or parts of the boundaries, of species' ranges with the boundaries of the water masses is often marked.

In proceeding from the Romanche Trench to Bermuda on Cruise 17, CHAIN necessarily crossed the boundary between the South Atlantic Central Water Mass and the North Atlantic Central Water Mass. Sverdrup, Johnson, and Fleming (1942: 669, fig. 183) show this boundary as a belt (presumably of transitional water) near 10°N, somewhat wider in the east than in the west and slightly concave to the north.

On May 3 and 4, 1961, as CHAIN traversed the parallels *ca.* 11°–15°N, it was recognized that the ship was in a region of transition. Changes were noted in the number and kinds of petrels, in both broad-band

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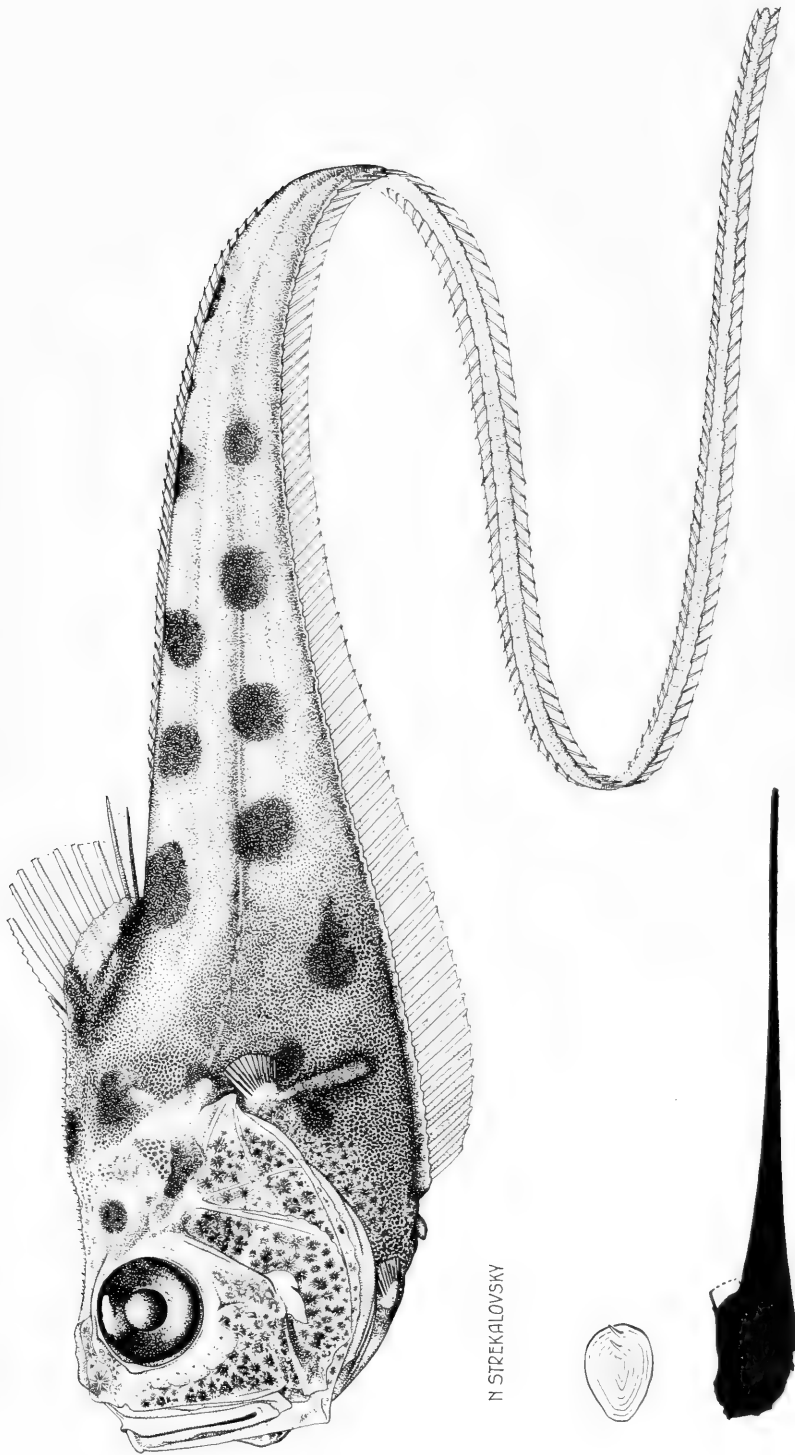
Fig. 3. ¿*Sphagemacrurus?* sp. 153 mm S. L.

and 12-kcps mid-water sound-scattering, in numbers of flying fish, in numbers of Portuguese Men-o'-War (*Physalia*), in water color, and in wind direction. With respect to 12-kcps sound-scattering, May 3 was recorded as a "sort of day of transition." After the cruise, measurements that had been made of other ocean properties were inspected for changes which had occurred on or about May 3. Among these, the change in the bathythermograph section was notable (Fig. 5).

For detecting faunal boundaries within the transect from Collection 800 to Collection 813, we have derived a method from the simple device of adding the number of species caught for the first time at a station, a_o, to those caught for the last time at the preceding station, b_o (Table 2, Cols. 2 and 4).[4] Freed of bias and with due allowance for sampling error, maxima of $a_o + b_o$ should occur at station intervals containing faunal boundaries if there be such.

It is evident, in sampling a homogeneous population, that the number of first-time and last-time captures of species in a collection will vary more or less directly as the total number of species in that collection. (This total number ranges from 7 to 35 in our 14 collections.) To minimize this bias we have divided each a_o and each b_o by the ratio of the number of species in the collection concerned (s) to the average such number ($\bar{s} = 21.0$) (Table 2, Cols. 3 and 5); a_o corr. for a collection is added to b_o corr. of the preceding collection to give a_o corr. $+ b_o$ corr. for the interval between collections (Table 2, Col. 6).

In sampling along a homogeneous transect, the chances of taking species for the first time must diminish steadily as the sampling proceeds (for instance, all species taken in the first collection necessarily are

[4] We experimented with adapting Simpson's (1960) index of faunal resemblance, C/N₁ × 100, to our needs but were not successful. C is the number of taxa common to two faunas being compared, while N_1 is the total number of taxa in the smaller of the two.

taken for the first time) and, conversely, the chances of taking species for the last time will increase steadily (all species taken in the last collection necessarily are taken for the last time). With this in mind we have constructed an expected distribution of first-time and last-time captures with successive samplings, assuming a homogeneous population along our transect.

These values were computed for a community of species that is most easily described by likening it to a community of numbers in an urn. Each number is represented once. Fourteen drawings (corresponding to the 14 CHAIN-17 collections) are made of 21 numbers each (corresponding to the average number of species in Collections 800–813). The numbers are replaced after each drawing. It is not necessary actually to engage in this drawing for the average result is described by the expression

$$a_c(x) = k - \frac{k}{N}\sum_{n=0}^{x-1} a_c(n) ,$$

where $a_c(x)$ is the number of first-time captures of numbers in drawing x, k is the number of numbers taken with each drawing, N is the number of numbers in the urn, and $\sum_{n=0}^{x-1} a_c(n)$ is the sum of first-captures from prior drawings. To make such a computation analogous to the capture of species in the CHAIN-17 collections, it was necessary to set $N = 128$ to insure that 118 (the total number of species in Collections 800–813) numbers had been taken after 14 drawings. The 14 successively computed values of a_c (Table 2, Col. 7) are plotted in Figure 6.

This model, in which all species are represented equally, admittedly does not describe realistically any natural community of species. To determine the amount of bias thus introduced, we have compared the distribution of first-captures of species in this simplified model with the distribution of first-captures empirically determined from a complex community of numbers in which all numbers (or species) are not

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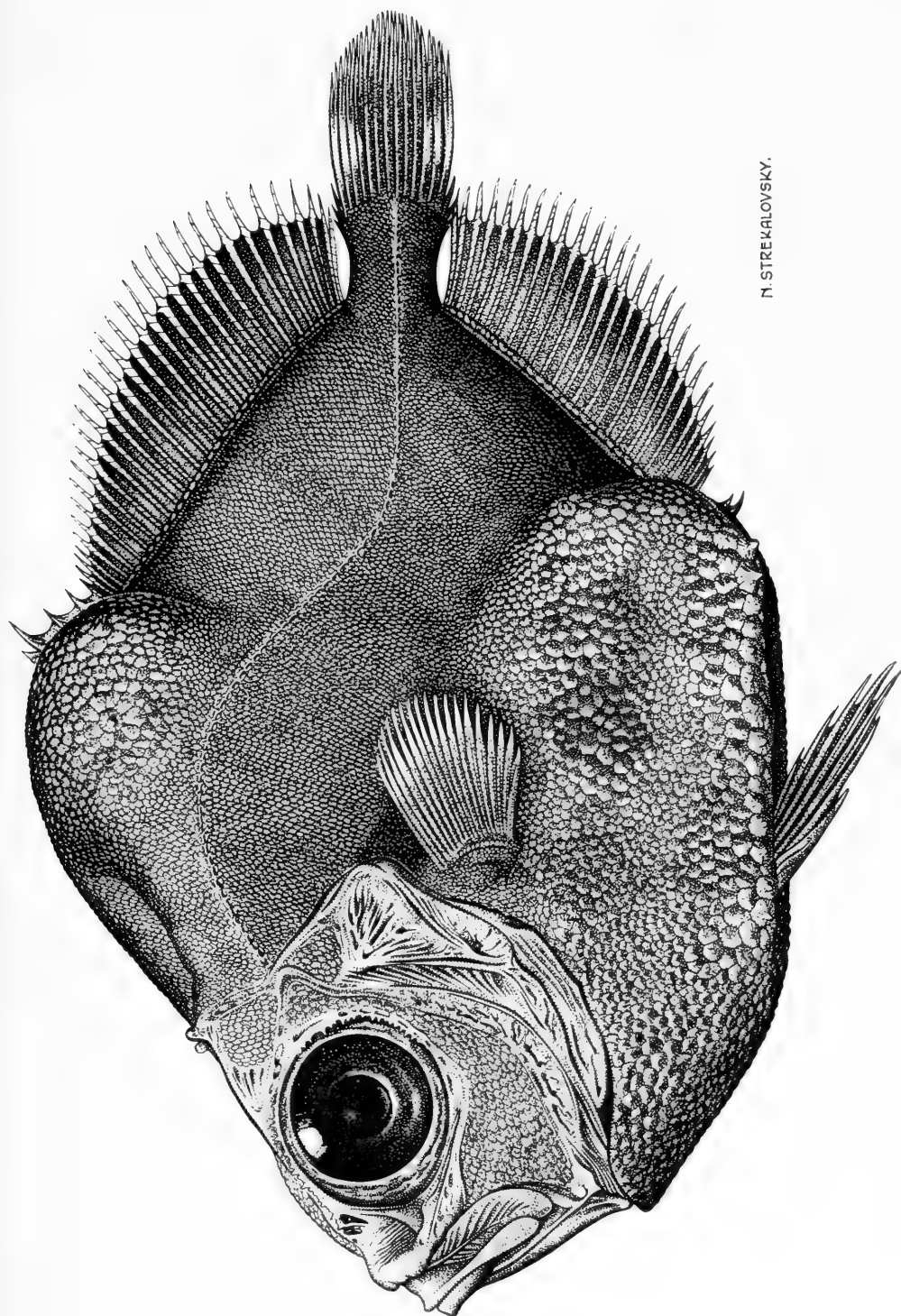
Fig. 4. *Neocyttus chelgae* (Holt and Byrne, 1908)? 72.5 mm S. L.
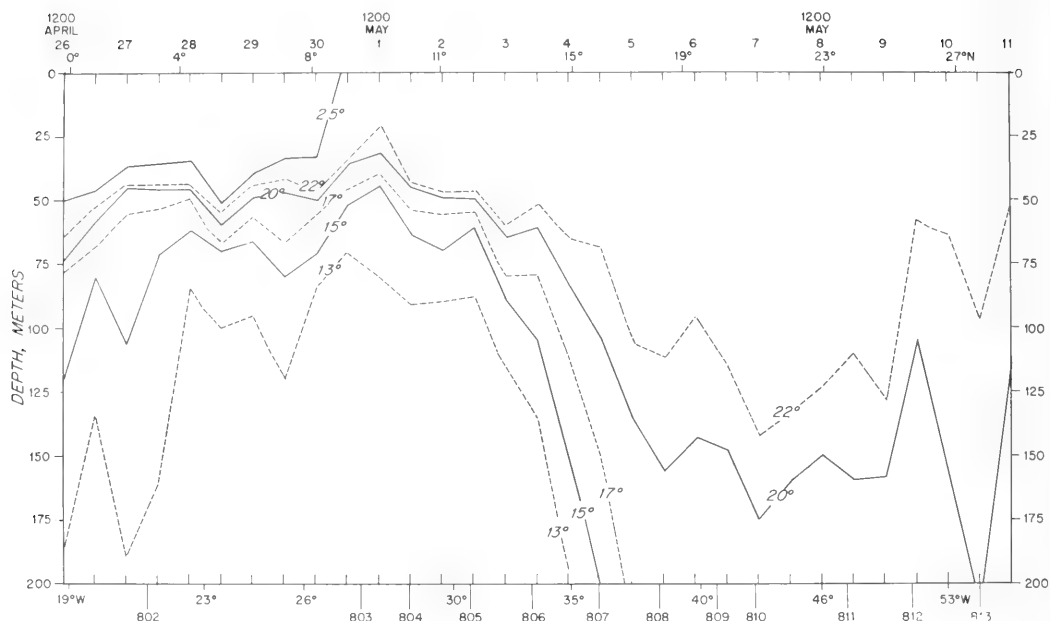
Fig. 5.   Temperature vs. depth along the collection transect constructed from bathythermograph observations.

represented equally. The incidence of numbers in this community was made to resemble the incidence (number of collections in which a species occurred) of species in the CHAIN-17 samples. Fourteen consecutive drawings of 23 numbers were made and the numbers of first-time captures noted with each successive drawing. (It was determined that 23 numbers were needed to be drawn to assure that, on the average, about 21 different ones would be drawn on the first sampling.) The whole procedure was repeated six times. Mean values from these six trials were calculated for first-time captures for samplings 1–14. These mean values are plotted in Figure 6 with a curve fitted by eye. Since this distribution of first-time captures does not differ greatly from that for the simpler model, since a number of poor assumptions must be made in the design of the community of numbers in the complex model, and since we have not been able to calculate (but must determine empirically) the distribution of first-time

captures in the complex one, we have contented ourselves with the simple distribution.

When the order of the a_c's computed from the simple model is reversed, the numbers correspond to 14 successive values of b_c, the expected number of last-time captures with successive samplings (Table 2, Col. 8). From a_c for a collection and b_c for the collection in arrears, the value $a_c + b_c$ was obtained for each collection interval (Table 2, Col. 9). Comparisons were then made *individually* between expected values for collection intervals and those observed, using the chi-square test and obtaining probability levels based on single degrees of freedom. The deviations of the observed from the expected values and the chi-square values are plotted against collection interval in Figure 7. Levels of significance are indicated for a single degree of freedom. The peak in the interval between Collections 807 and 808 ($x^2 = 3.79$) implies a faunal boundary, for here the odds are
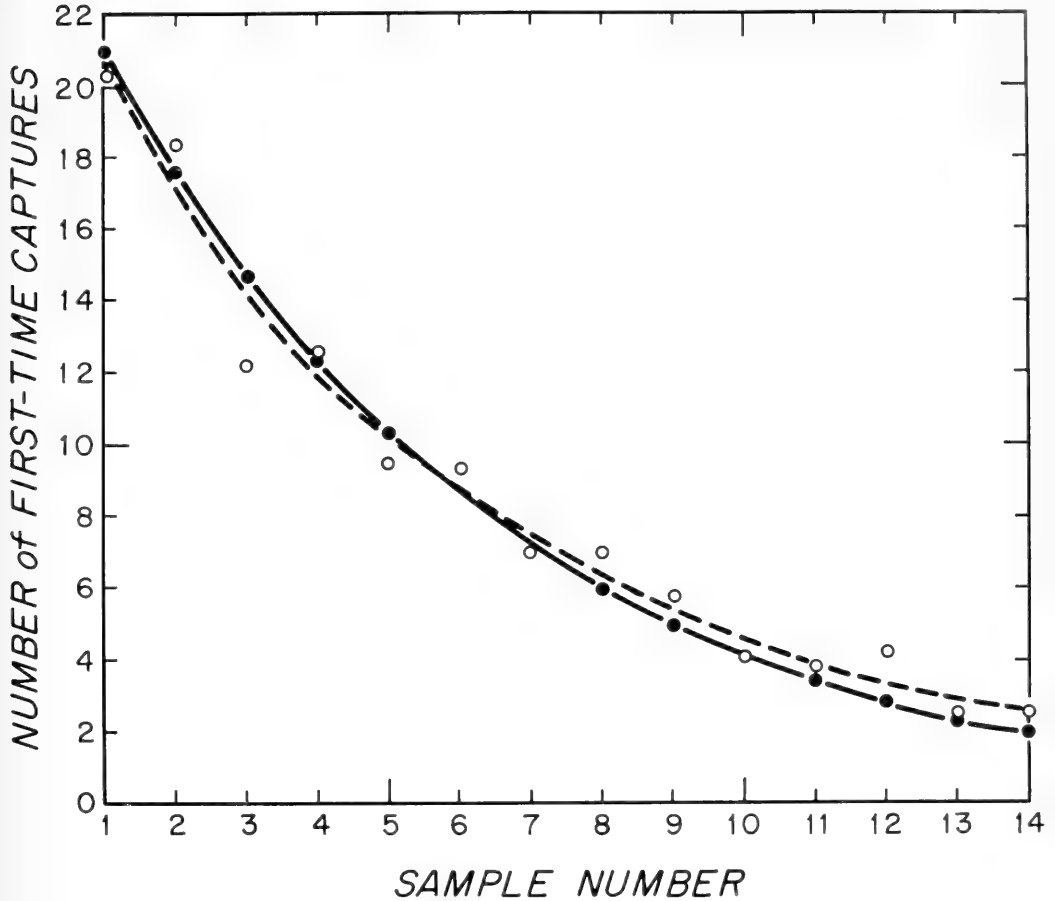
Fig. 6. Frequency of first-time captures with successive samples. Filled circles are values computed from population in which all species are represented once, open circles empirically determined from population with species not represented equally. See text.

about 19 to 1 that the departure of the observed from the expected is not due simply to sampling error. The value for the interval 806–807 is also significant (P < .10), suggesting that the boundary is not an abrupt one.

Additional evidence for a faunal boundary near the site of Collection 807 is the difference in faunal diversity in Collections 800–806 and Collections 807–813. Table 1 and Figure 8 show that there is a pronounced break in the number of species per collection between Collections 806 and 807

without a similar pattern in the number of specimens per collection. The fauna south of the boundary is markedly more diverse. For Collections 800–806, $\bar{x} = 28.1$, $s = 6.62$, and $s_{\bar{x}} = 2.50$. For Collections 807–813, $\bar{x} = 13.8$, $s = 3.48$, and $s_{\bar{x}} = 1.31$.

The faunal boundary indicated around Collection 807 occurs just after an abrupt deepening and diverging of the 20° and 15° isotherms (Fig. 5). Previously, the two isotherms had been close to one another in a layer between about 25 and 100 meters. This sudden degradation of the thermocline
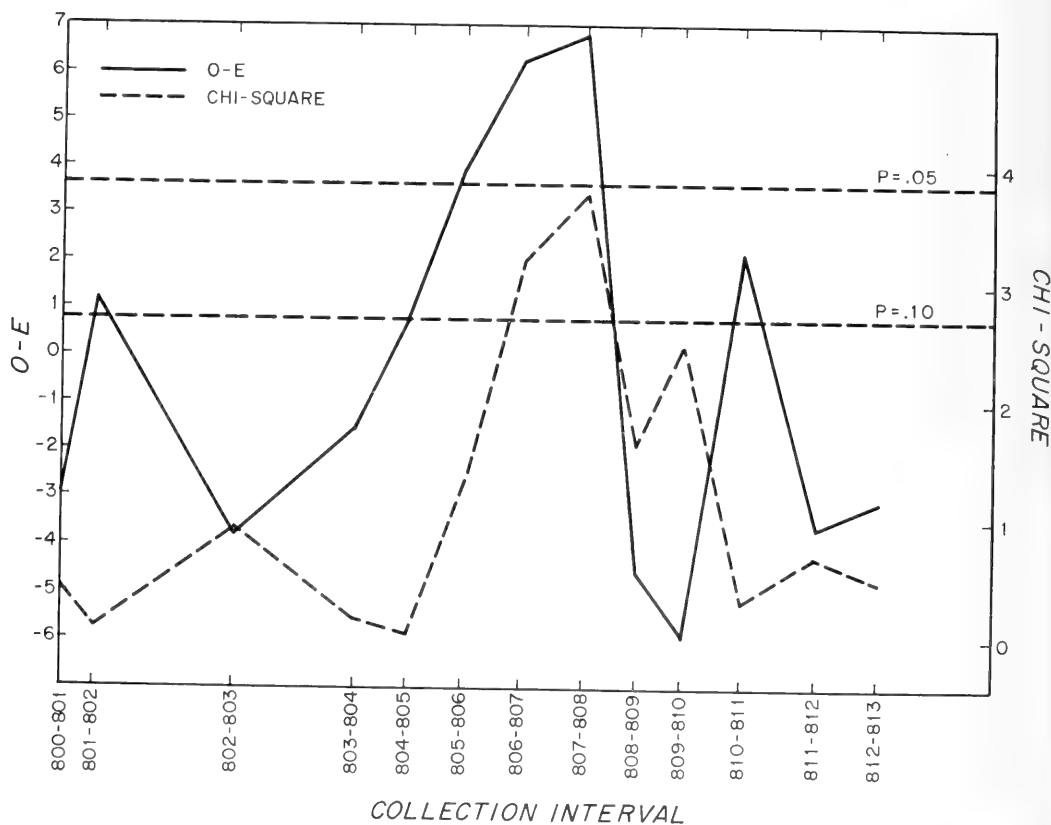
Fig. 7. The deviations of expected first-time captures from the observed first-time captures for the several collections and the chi-square values calculated from them. Probability levels for comparing with the chi-square values are shown also. See text.

and thickening of the surface isothermal (or near-isothermal) layer with increasing latitude can be noted in other corresponding sections, e.g., near 15°N, 50°W in a November-December section of ATLANTIS (Fuglister, 1960); near 12°N, 30°W in an April-May section of MIKHAIL LOMONOSOV (Gamutilov and Gruzinov, 1960); and near 12°N, 41°W in a March section of ATLANTIS (Iselin, 1936), and hence is considered a permanent feature in this part of the ocean.

To better understand this marked phenomenon we have made a temperature-salinity plot of observations at ATLANTIS stations 1177–1165 from the March section noted above (Fig. 9). Stations 1177–1172 (*ca.* 3°N–12°N) were dominated in their upper levels by South Atlantic Central Water. Temperatures at 200 meters ranged from 9.7°C to 12.5°C (excepting one of 13.9°C at 3°N, far removed from the region of our interest). Stations 1169–1165 (*ca.* 16°30′N–22°30′N) were dominated in their upper levels by North Atlantic Central Water. Temperatures at 200 meters ranged from 17.2°C to 19.6°C. Stations 1171 (*ca.* 13°30′N) and 1170 (*ca.* 15°N) were intermediate in nature and had 200-meter temperatures of 14.2°C and 15.3°C respectively.

Thus, the BT section and T-S diagram together show that the faunal boundary near Collection 807 corresponds to the boundary between the South Atlantic Cen-
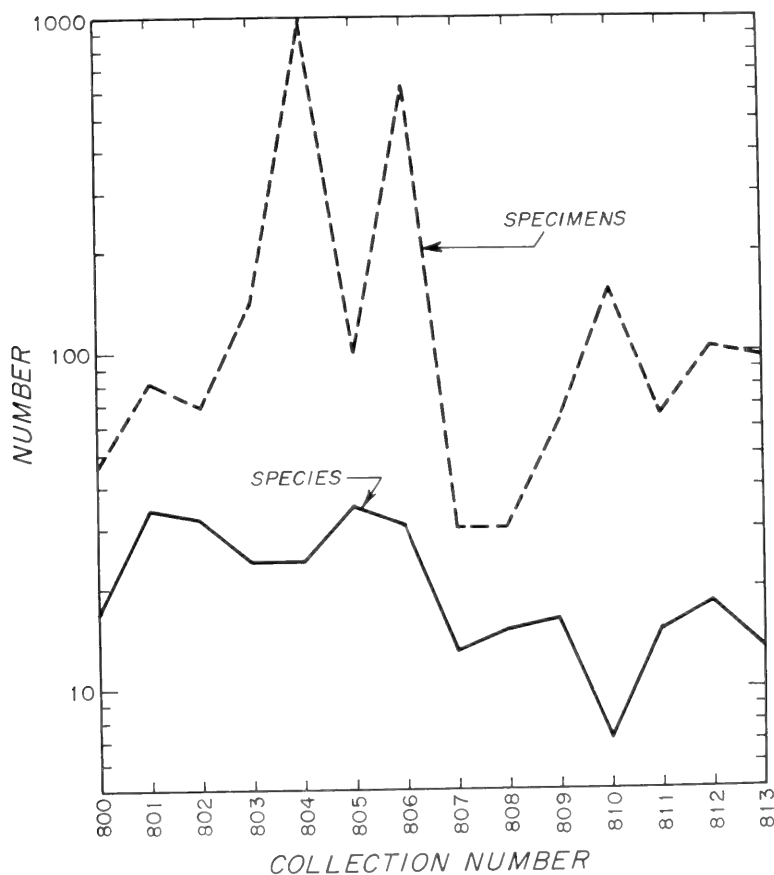
Fig. 8.   Numbers of species and specimens per collection for each of Collections 800–813.

tral Water and North Atlantic Central Water Masses. A good working rule would seem to be that when the 200-meter temperature in these latitudes is in excess of about 15°C, the observer is in the North Atlantic Central Water Mass; when the 200-meter temperature is less than about 13°C, the observer is in the South Atlantic Central Water Mass. Isotherms for these temperatures at the 200-meter level are given by Schroeder (1963) and her plate 4 should be of great use to zoogeographers working in this area.

Although the boundary noted marks the meeting of the North and South Atlantic Central Water Masses, it is not, in terms of circulation, the meeting of the central gyres of these two oceans. These gyres are separated by an equatorial zone defined by the shallow thermocline of steep gradient already noted ("the well-known equatorial discontinuity layer," Voorhis, 1961). The degradation of this layer can be said to mark the poleward limits of the equatorial zone. To the north, the boundary of this zone and the boundary between North and South Atlantic Central Water Masses are thus co-determined. Does this boundary have faunal significance because it marks the northern edge of the equatorial zone or because it marks the meeting of North and South Atlantic Central Water Masses? For the time being we must beg the question. It can be approached by determining, when collections are available, the faunal
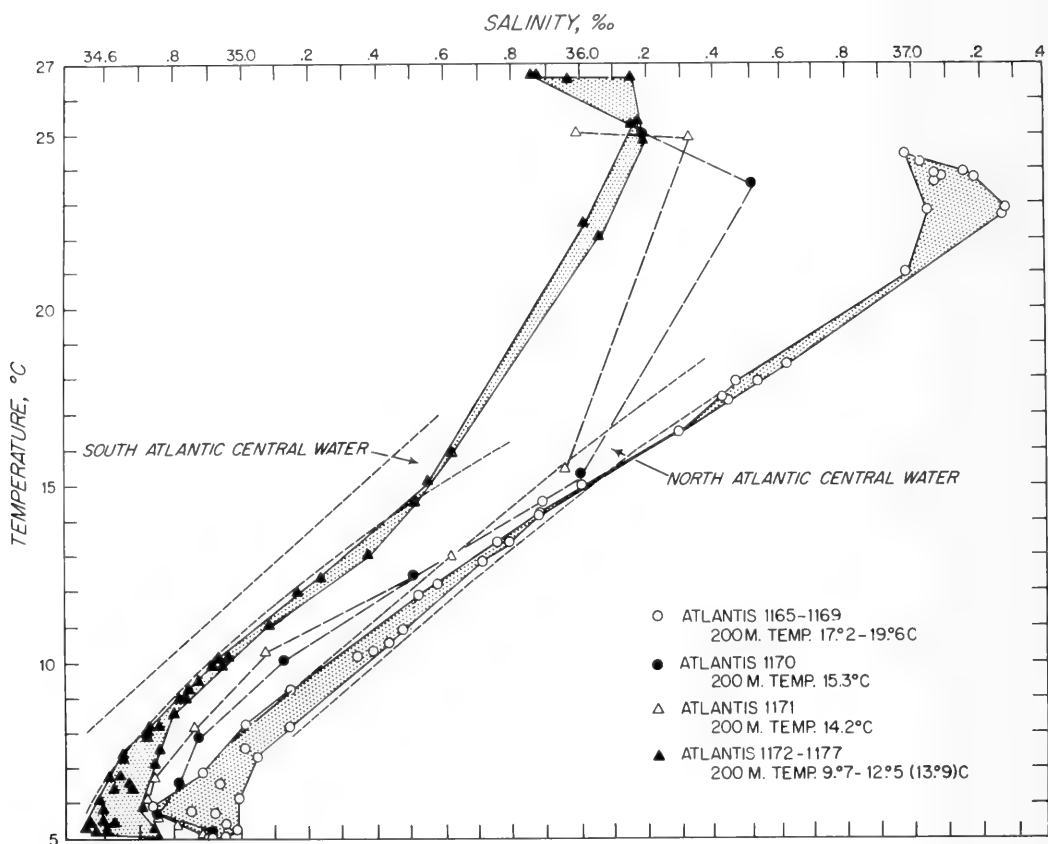
Fig. 9. Temperature-salinity relationships for North Atlantic Central Water and South Atlantic Central Water and the relationship of these to 200-m temperatures in the southern North Atlantic.

significance of the boundary between the equatorial zone and the South Atlantic central gyre.

What is the relation of the boundary noted near Collection 807 (*ca.* 16°N) to the southern edge of the Sargasso Sea? Recent physical definitions of the Sargasso Sea have been based on the distribution of superabundances of 18° water (Worthington, 1959, and Istoshin, 1961). The Sargasso Sea so defined, in general finds its southern edge at about 20°N.[5] Judging

from Worthington's chart, CHAIN crossed this boundary at about 21°–22°N, 45°W (between Collections 810 and 811). Analysis of our data by the method of first-plus-last captures gives no indication of a boundary here, although the collection lists show that the myctophids *Lampanyctus cuprarius*, *Lampanyctus photonotus*, and *Lepidophanes gaussi* occur primarily in the Sargasso Sea collections (see Table 3). *Melamphaes pumilus* Ebeling is an example of a fish whose range conforms closely to Worthing-

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[5] Worthington's and Istoshin's Sargasso Seas are derived by somewhat different methods, though both are based on the superabundance of 18° water. The geographical limits of their seas conform quite closely. Winge's (1923) Sargasso Sea,

based on the distribution of *Sargassum* and therefore having semantics on its side, fits the others well enough except that it extends much farther to the east (to 30°W or more, while the others reach only to about 40°W).

ton's and Istoshin's Sargasso Sea (Ebeling, 1962). It should be noted that our collections are not sufficient for denying the existence of boundaries (especially weakly developed ones), which is quite a different matter from *establishing* the existence of strong ones.

Table 3 shows the occurrence of all species that were taken three or more times in Collections 800–813, plus certain additional species in *Chauliodus* and *Lampanyctus*. Some species that are confined to the southern end of our transect are known to be widely distributed well to the north of our northernmost collection. An example is *Diaphus dofleini,* which is the commonest mesopelagic myctophid in the slope water off southern New England (Hersey and Backus, 1954) and is widely distributed in the northeastern Atlantic (Bolin, 1959). It appears to be replaced by its sibling, *Diaphus gemellari,* in the central North Atlantic. Perhaps this is an example of a species pair in which one species is found in areas of high productivity, the other in poorer areas (Ebeling, 1962), although such a distribution may prove explainable on the basis of temperature alone, with *D. gemellari* confined to warmer waters. The upper part of the mesopelagial in the North Atlantic does not cool from the equator polewards; rather, it cools both equatorwards and polewards from a line connecting Guatemala in the west (*ca.* 15°N) with the Canary Islands in the east (*ca.* 28°N) (Schroeder, 1963). This fact of the physical environment of the North Atlantic generally has been overlooked in discussing disjunct ranges of mesopelagic animals.

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TABLE 2. VALUES FOR COLLECTIONS AND TRANSECT COLLECTION-INTERVALS USED IN THE ANALYSIS FOR FAUNAL BOUNDARY

1 COLLEC-TION	2 a_o	3 a_o CORR.	4 b_o	5 b_o CORR.	6 a_o CORR. + b_o CORR.	7 a_t	8 b_t	9 $a_t + b_t$	10 $O - E$	11 χ^2
800	17	21.0	2	2.5		21.0	2.0			
					16.7			19.6	−2.9	0.429
801	23	14.2	10	6.2		17.6	2.4			
					19.3			18.1	1.2	0.080
802	20	13.1	8	5.3		14.7	2.9			
					11.4			15.2	−3.8	0.947
803	7	6.1	5	4.4		12.3	3.5			
					12.3			13.8	−1.5	0.163
804	9	7.9	6	5.2		10.3	4.2			
					13.6			12.8	0.8	0.050
805	14	8.4	18	10.8		8.6	5.0			
					16.2			12.2	4.0	1.311
806	8	5.4	15	10.2		7.2	6.0			
					18.3			12.0	6.3	3.233
807	5	8.1	10	16.2		6.0	7.2			
					19.0			12.2	6.8	3.787
808	2	2.8	4	5.6		5.0	8.6			
					8.2			12.8	−4.6	1.656
809	2	2.6	6	7.9		4.2	10.3			
					7.9			13.8	−5.9	2.522
810	0	0	4	12.0		3.5	12.3			
					17.6			15.2	2.2	0.318
811	4	5.6	7	9.8		2.9	14.7			
					14.5			18.1	−3.6	0.718
812	4	4.7	10	11.7		2.4	17.6			
					16.5			19.6	−3.1	0.490
813	3	4.8	13	21.0		2.0	21.0			

Table 3. Number of specimens of certain species in collections 800–813

	800	801	802	803	804	805	806	807	808	809	810	811	812	813
Argyropelecus aculeatus						14	–	–	2	–	1			
Argyropelecus lychnus			1	3	–	3	–	3						
Bathysphyraenops simplex	6	–	1	–	–	–	1							
Benthosema suborbitale					5	–	122	–	4	4	–	1	3	
Bonapartia pedaliota			9	32	–	2								
Ceratoscopelus townsendi	1	1	–	–	27	–	25	–	1	5	–	5	14	12
Chauliodus danae								2	4	–	–	1		
Chauliodus schmidti				2	1									
Chauliodus sloani		1												
Cyclothone sp. A			1	5	–	1	–	–	1	–	145	5		
Diaphus brachycephalus	2	13	–	–	–	–	–	–	1					
Diaphus dofleini		1	–	3	1									
Diaphus fragilis	1	1	–	–	–	–	53	–	–	4				
Diaphus gemellari							5	–	5	1	1	3	1	
Diaphus lucidus	1	1	1	–	–	1								
Diaphus luetkeni	2	1	11	3	5	2	10	1						
Diaphus mollis	1	–	–	–	1	–	12	–	–	2	1	–	7	5
Diaphus problematicus	1	–	–	–	–	–	–	–	1	–	–	1		
Diaphus sp. A		1	–	3	94									
Diogenichthys atlanticus		1	–	1	87	–	65							
Diretmus argenteus		3	–	7	–	19								
Evermannella indica						2	–	–	–	–		–	1	2
Gonostoma atlanticum			6	18	–	4								
Gonostoma sp. A	1	–	–	–	–	1	18							
Hygophum macrochir		13	–	1	69	1	3	–	–	2				
Hygophum reinhardti				1	1	–	1	–	1	–	–	–	2	
Ichthyococcus ovatus			3	6	–	1	4							
Isistius brasiliensis		1	1	–	–	1								
Lampanyctus alatus	4	4	1	–	–	–	4							
Lampanyctus cuprarius													9	2
Lampanyctus ¿lineatus?						5								
Lampanyctus macropterus	3	4	3	–	–	–	–	–	–	9				
Lampanyctus photonotus		1	–	–	–	–	–	–	–	13	–	25	9	21
Lepidophanes gaussi										2	–	12	5	10
Lepidophanes guentheri		5	2	9	71	–	4	–	2	–	–	1	–	2
Lepidophanes pyrsobolus							1	1	1	3	–	2	7	8
Nemichthys scolopaceus			1	–	–	1	–	1						
Notolychnus valdiviae				5	39	–	94	–	–	6	–	–	27	21
Notoscopelus resplendens		1	–	1	101	1	31							
Scopelogadus mizolepis	1	1	1	2	–	16								
Stomias affinis			3	–	4	–	1							
Valenciennellus tripunctulatus			4	2	–	1	–	9	4	–	3			
Vinciguerria nimbaria	16	8	1	31	159	–	100	–	–	7	–	1		
Vinciguerria sp. A					245	1	28	–	–	–	2			

New Species of *Hemicyclops* (Copepoda, Cyclopoida) from Madagascar

by ARTHUR G. HUMES

NEW SPECIES OF *HEMICYCLOPS* (COPEPODA, CYCLOPOIDA) FROM MADAGASCAR

ARTHUR G. HUMES[1]

INTRODUCTION

One species of the genus *Hemicyclops*, *H. visendus* Humes, Cressey, and Gooding, 1958, is already known from Madagascar. This copepod lives at Nosy Bé in association with the thalassinidean shrimp *Upogebia* (*Upogebia*) sp., having been recovered by washing the bodies of the crustaceans in sea water with a small amount of ethyl alcohol.

As a result of extensive collecting in the region of Nosy Bé during 1960 and 1963–64, seven more species of *Hemicyclops* have been found, all of them new. Two of the species came from burrows known to be inhabited by a shrimp, one was washed from the body of a stomatopod, and the remaining four were recovered from water drawn from intertidal burrows of unknown origin by means of a small hand-operated bilge pump.

The island of Nosy Bé lies a few miles off the northwestern coast of Madagascar and is intersected by Lat. 13°20′S and Long. 48°15′E. (The map presented by Humes, 1962, p. 39, shows a French geographic grid based on a circle of 400°, with the longitude relative to the Paris meridian, instead of the more conventional degrees of latitude and longitude.) The spelling "Nosy Bé" (nosy = island, and bé = large, in Malgache) is the preferred form, although "Nossi Bé" is sometimes used.

The material covered in this work comprises copepods from (1) burrows of the thalassinidean shrimp *Axius* (*Neaxius*) *acanthus* A. Milne Edwards:

> *Hemicyclops axiophilus* n. sp.
> *Hemicyclops amplicaudatus* n. sp.

(2) burrows of unknown origin:

> *Hemicyclops carinifer* n. sp.
> *Hemicyclops diremptus* n. sp.
> *Hemicyclops kombensis* n. sp.
> *Hemicyclops biflagellatus* n. sp.

(3) the body of the stomatopod crustacean *Acanthosquilla* sp.:

> *Hemicyclops acanthosquillae* n. sp.

[1] Boston University, Boston, Mass., and Associate in Marine Invertebrates, Museum of Comparative Zoology.

SYSTEMATIC DESCRIPTION

Hemicyclops axiophilus[1] n. sp.

Pls. I–VI; VII, figs. 39–40

Type material.—276 females, 282 males, and about 100 copepodids from water in the burrows of the thalassinidean crustacean *Axius* (*Neaxius*) *acanthus* A. Milne Edwards (determined by Dr. Fenner A. Chace, Jr.) in sand exposed at low tide at the northeastern end of the beach at Andilana (sometimes spelled Andilah), on the northern side of Nosy Bé, Madagascar. Collected by A. G. Humes September 4, 1960. Holotype female, allotype, and 110 paratypes (55 of each sex) deposited in the United States National Museum, Washington; the same number of paratypes in the Muséum National d'Histoire Naturelle, Paris, the British Museum (Natural History), London, and the Museum of Comparative Zoology, Cambridge, Mass. The remaining paratypes are in the collection of the author.

Other specimens (from burrows presumed to be of the same host).—68 females, 64 males, and 30 copepodids along the southwestern shore of Nosy Iranja, about 55 kilometers southwest of Nosy Bé, September 7, 1960; 26 females, 6 males, and 3 copepodids in the same locality, October 7, 1960; 12 females, 9 males, and 3 copepodids at Andilana, October 8, 1960; 93 females, 96 males, and 3 copepodids at Andilana, August 8, 1960; 98 females, 47 males, and 3 copepodids at Nosy Iranja, November 4, 1963; 38 females, 60 males, and 40 copepodids at Antsakoabe, east of Andilana, November 1, 1963; 50 females, 41 males, and 22 copepodids at Navetsy, on the northernmost end of Nosy Bé, November 3, 1963; 19 females, 26 males, and 19 copepodids from Nosy N'Tangam, near Dzamandzar, Nosy Bé, December 2, 1963; and 97 females, 37 males, and 11 copepodids from the same locality, January 1, 1964.

Female.—The body length (not including the setae on the caudal rami) is 1.80 mm

[1] The specific name *axiophilus* is derived from *Axius*, the generic name of the crustacean with which the copepod is associated, and φιλος, loving.

(1.66–1.89 mm) and the greatest width (near the posterior edge of the cephalosome) is 0.79 mm (0.70–0.86 mm), based on 10 individuals. The prosome is a little longer than the urosome, the ratio being about 1.4 : 1 (Fig. 1). The tergal plates of pedigerous segments 1–4 (Fig. 2) are well separated laterally (with acute posterolateral angles) and are ornamented, like the rest of the dorsal surface of the prosome, with small knobs and hairs. The segment of leg 5 is smaller, without produced epimera and with two groups of rather long hairs on the dorsolateral areas. An almost complete intersegmental sclerite occurs between this segment and the next. The genital segment (Fig. 3) is about 310 μ in length, without a trace of division into its two constituent somites. It is broadest in its anterior third (268 μ), has a moderate ventrolateral expansion in its middle third (211 μ), and is narrowest in its posterior third (169 μ), where the sides are nearly parallel. There is an extensive lateral invagination between the anterior and middle thirds. Details of the border of the anterior two-thirds of the genital segment are shown in Figures 4 and 5. The egg sacs are attached dorsolaterally on the anterior part of the broadened anterior third. Near the attachment of each sac there are two minute blunt spines, each about 9 μ in length (Fig. 6); posterior to the attachment area there is a single isolated small seta. Each egg sac is oval, about 507 × 253 μ (based on 3 individuals), and contains many small eggs (Fig. 1).

The spermatophores when attached to the female are carried along the posterior third of the genital segment (Fig. 1), behind the middle expansion. The three postgenital segments (Fig. 3) measure in length, respectively, 122, 96, and 72 μ, the last of these segments with a row of minute spinules on the ventral posterior margin near the insertion of the ramus. A row of smaller spinules continues laterally on the ventral posterior margin (see Fig. 7). Two diagonal rows of very fine spinules form a V on the dorsal anal area. A few minute refractile points

occur on the ventral surface of the first post-genital somite.

The caudal ramus (Fig. 7) measures $102 \times 53\,\mu$ (2.0 times longer than wide), based on 5 individuals, the length measured ventrally along the inner edge. The lateral seta is $88\,\mu$ in length, without hairs or spinules, but with a narrow flange along the posterior edge. The dorsal seta is $100\,\mu$ long and haired. The innermost terminal seta is $226\,\mu$ long, with erect lateral hairs; the outermost terminal seta is $83\,\mu$ long, naked, with the proximal two-thirds having an inner flange and terminating in two pointed processes, the distal third forming a hyaline flagellum (Fig. 8). Of the two long terminal setae, the outer one is $437\,\mu$ in length, the inner one $728\,\mu$, both with a basal peg and with lateral hairs. A minute hyaline setule (hair?) occurs on the outer edge near the base of the ramus. There is a row of long setules along the distal half of the inner edge, and a small group of spinules at the inner distal corner of the ramus. The distal end of the ramus overlaps ventrally the insertions of the four terminal setae.

The rostral area (Fig. 9) bears two small hairs and a few refractile points.

The first antenna (Fig. 10) has 7 segments, their lengths (measured along their forward setiferous margins) beginning at the base: 56, 94, 55, 117, 62, 53, and $52\,\mu$, respectively. The first segment bears 4 setae, the second 15 (some of them apparently with extremely short lateral hairs in their proximal halves), the third 6, the fourth 3, the fifth 4 and 1 aesthete, the sixth 2 and 1 aesthete, and the seventh 7 and 1 aesthete. All but 6 setae are annulate, these six being disposed as follows: 1 each on segments 5 and 6, 4 on the terminal segment. On the distal anterodorsal surface of the second segment there are a few transverse refractile lines as shown in the figure.

The second antenna (Fig. 11) is 4-segmented, with the third segment produced on the inner distal corner and bearing there 2 spines, the proximal one blunt and having a spinulose flange, the distal one attenuated

and bearing a row of spinules, both spines with a subterminal setule. The fourth segment measures about $36 \times 29\,\mu$ and has 3 hyaline, pectinate flanges, two on the outer side and one on its posterior surface. The remaining armature and ornamentation is shown in the figure.

The labrum in anterior (dorsal) view (Fig. 12) is slightly trilobed with a row of 5–10 setules along its free edge. In posterior (ventral) view (Fig. 13) the labrum has a complex ornamentation, as shown in the figure.

The metastomal areas have the ornamentation indicated in Figure 14, with the anterior area showing mostly hairs, the posterior one bearing spinules.

The mandible (Fig. 15) has the usual two stout elements and two spinulose setae. The paragnath (Fig. 16) is a large lobe bearing spinules and hairs. The first maxilla (Fig. 17), the second maxilla (Fig. 18), and the maxilliped (Fig. 19) present no outstanding differences from other species. Seen ventrally, the maxillipeds are connected by a line (Fig. 20) probably representing a trace of an intercoxal plate. The postoral protuberance is neither well defined nor particularly well developed.

The armature of legs 1–4 (Figs. 21, 22, 23, and 24) is as follows (the Roman numerals representing the spines, the Arabic numerals the setae):

P1	protopod	0:1	1:1	exp	I:0	I:1	I,7
				end	0:1	0:1	I,5
P2	protopod	0:1	1:0	exp	I:0	I:1	II,7
				end	0:1	0:2	I,II,3
P3	protopod	0:1	1:0	exp	I:0	I:1	II,7
				end	0:1	0:2	I,II,3
P4	protopod	0:1	1:0	exp	I:0	I:1	I,7
				end	0:1	0:2	I,II,2

The formula for the terminal segments of the exopods and endopods depends in some cases upon whether an element is interpreted as a "spine" or a "seta." Thus, when comparing the armature of the legs, reference should also be made to the figures.

Leg 1 bears on its basis an inner spine $70\,\mu$ in length, and its exopod spines have subterminal setules; both of these features

being absent on legs 2–4. On leg 3 the distalmost of the three spines on the last exopod segment is somewhat intermediate in form between a spine and a seta, and the distalmost of the three spines on the last endopod segment is nearly twice the length of the other two (48, 49, and 95 μ, respectively). The spines on all four legs have slight spinulose flanges.

Leg 5 (Figs. 25 and 26) has a rather short and broad free segment, measuring 134 × 84 μ (based on 4 specimens), or about 1.6 times longer than wide. There are rows of spinules on both outer and inner margins. The three terminal spines are 60, 57, and 68 μ in length, respectively, from outer to inner, and the terminal seta is 104 μ long. (One female from Nosy Iranja showed a normal right leg, but the left leg 5 was abnormal, lacking the innermost terminal spine and having a smooth inner margin on the free segment.) The seta arising from the body near the base of the free segment is about as long as the free segment. The area adjacent to the insertion of the free segment of leg 5 is ornamented with groups of slender setules and spines, as shown in the figures.

Leg 6 is apparently absent.

The color in living specimens in transmitted light includes red speckling along the sides of the prosome, a red eye, a gray ovary, and orange-red to gray egg sacs.

Male.—The body length (not including the setae on the caudal rami) is 1.57 mm (1.44–1.73 mm), and the greatest width is 0.67 mm (0.61–0.77 mm), based on 10 individuals. The body form (Fig. 27) in general resembles that of the female, with a similar ratio of prosome to urosome. The tergum of the fifth pedigerous segment appears to be not as clearly defined as in the female and lacks the two groups of hairs near the insertion of leg 5. The genital segment in dorsal or ventral outline is subcircular (Fig. 28), 190 μ long and 247 μ wide. The four postgenital segments are 125, 104, 72, and 62 μ in length, respectively. A few scattered refractile points and hairs may be seen on the dorsal surface of the

genital and postgenital segments, as shown in the figure.

The caudal ramus is similar to that of the female but a little shorter, its average size (based on 5 individuals) being 88 × 51 μ, or about 1.7 times longer than wide.

The spermatophore attached to the body of the female (Fig. 29) is pyriform, 99 × 70 μ, not including the short neck; the spermatophore seen inside the body of the male (Fig. 30) appears to be a little smaller (86 × 62 μ).

The rostral area is like that of the female.

The first antenna is similar to that of the female, but there is an additional seta on the third and fourth segments (Fig. 31), so that the formula for the seven segments is: 4, 15, 7, 4, 4 + 1 aesthete, 2 + 1 aesthete, and 7 + 1 aesthete.

The second antenna resembles that of the female.

The labrum (Fig. 32) lacks the line of long setules on its anterior surface and shows a more extensive area of fine, close-set spinules medially below the free ventral edge (replacing the two rows of spinules in the female). The second metastomal area has only one row of blunt triangular spines (instead of two as in the female).

The mandible, paragnath, and first maxilla are similar to those of the female. The second maxilla (Fig. 33) shows the stout inner spine on the second segment here replaced by a strongly sclerotized, claw-like element lacking an articulation with the segment. The details of the compound element are also slightly modified (Fig. 34).

The maxilliped (Figs. 35, 36, and 37) has a single seta on the first segment. The proximal inner angle of the second segment is greatly expanded, the segment being 190 μ along its outer margin and 169 μ in greatest width. There are three rows of blunt spinules and two setae on the inner surface of this segment. It also shows three groups of cuticular furrows on its inner posterior surface, as indicated in Figure 36. The third segment is very short and unarmed. The fourth segment extends into a long claw 260 μ in length (measured along its axis and

not along the curvature) bearing near its base a slender setiform process, a slender seta, and a minute setule.

Leg 1 lacks the inner spine on the basis (Fig. 38); otherwise legs 1–4 are similar to those of the female, with the same armature.

Leg 5 (Fig. 39) has a free segment more slender than in the female, measuring about 138×68 μ, or about 2 times longer than wide, with its armature resembling that in the female (the three spines are 70, 68, and 74 μ in length from outer to inner, the seta 83 μ long). The processes at the outer sides of the bases of the two proximal spines are larger than in the female. The seta arising from the body near the base of the free segment is shorter than the segment; near this seta there is a row of spinules, but the group of slender setules seen in the female is absent.

Leg 6 (Fig. 40) consists of a sclerotized flap bearing laterally a seta 64 μ in length. The sclerotizations on the segment, against which these flaps fit, are particularly heavy.

The color in living specimens resembles that of the female.

Remarks on its biology.—*H. axiophilus* was found in water in the relatively small burrows of *Axius acanthus* but never in burrows of larger size and presumed to be inhabited by other animals. (In every collection of *H. axiophilus* the copepod next described also occurred.) It seems to show a distinct preference for the burrows of *Axius* in the Nosy Bé region. The copepod apparently lives in the burrow water and not on the body of *Axius*, since no copepods were found on the bodies of 16 *Axius* dug from their burrows. All specimens were recovered by drawing water from the burrows by means of a small bilge pump.

In artificial lighting under a binocular microscope, the copepods showed a fairly strong positive photokinesis, with the majority of them concentrating on the side of the dish nearest the light source.

Two specimens (one female and one male) were observed whose intestines con-tained fragments of copepods, suggesting that in part at least the food of *H. axiophilus* includes copepods.

Relationship to other species.—*H. axiophilus* belongs to the group of species in the genus *Hemicyclops* having four setae on the first segment of the first antenna and a short terminal segment on the second antenna. It seems to be closest to *H. visendus* Humes, Cressey, and Gooding, 1958 (found associated with *Upogebia* at Nosy Bé). It differs from that species, however, in several respects. In the female of *H. visendus* the caudal ramus is about 1.7 times longer than wide, a rather large number of the setae on the first antenna have conspicuous lateral hairs, and the genital segment does not show two lateral expansions; in the male the body length is 2.06 mm, the genital segment is subrectangular in dorsal or ventral outline rather than subcircular, the second segment of the maxilliped is pyriform in outline rather than subtriangular, and the free segment of leg 5 is elongate, being 2.4 times longer than wide.

Hemicyclops amplicaudatus[1] n. sp.

Pl. VII, figs. 41–46; Pls. VIII–X; Pl. XI, figs. 71–72

Type material.—7 females and 17 males from water in burrows of *Axius* (*Neaxius*) *acanthus* A. Milne Edwards (determined by Dr. Fenner A. Chace, Jr.) in sand exposed at low tide along the southwestern shore of Nosy Iranja, about 55 kilometers southwest of Nosy Bé, Madagascar. Collected by A. G. Humes September 7, 1960. Holotype female, allotype, and 11 paratypes (2 females and 9 males) deposited in the United States National Museum, Washington; 6 paratypes (1 female and 5 males) in the Museum of Comparative Zoology, Cambridge, Mass.; and the remaining paratypes in the collection of the author.

Other specimens (from burrows pre-

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[1] The specific name *amplicaudatus*, from Latin *amplus* = wide, broad, and *cauda* = tail, refers to the unusually wide genital segment in this species.

sumed to be of the same host). — 13 females and 13 males on the northeastern end of the beach at Andilana, on the northern side of Nosy Bé, September 4, 1960; 7 females from the same locality, October 8, 1960; 11 females, 3 males, and 1 copepodid again from the same locality, August 8, 1963; 9 females and 1 male from Nosy Iranja, November 4, 1963; 9 females and 1 male from Antsakoabe, east of Andilana, November 1, 1963; 6 females and 5 males from Navetsy, on the northernmost end of Nosy Bé, November 3, 1963; 30 females and 21 males from Nosy N'Tangam, near Dzamandzar, Nosy Bé, January 1, 1964; and 10 females and 2 males from the same locality, December 2, 1963.

Female.—The length of the body (not including the setae on the caudal rami) is 1.34 mm (1.24–1.42 mm), and the greatest width (in the posterior third of the cephalosome) is 0.57 mm (0.53–0.62 mm), based on 10 individuals. The prosome is distinctly longer than the urosome (Fig. 41), the ratio being about 1.5 : 1. The epimera of pedigerous segments 1–4 are laterally somewhat rounded and closely imbricate, those of the segment bearing leg 4 partly covered by the tergal area of the preceding segment. The dorsal surface of the prosome bears scattered hairs mounted on refractile points; these hairs extend around onto the ventral edges of the cephalosome (Fig. 42). The segment bearing leg 5 has dorsally two raised lobes, each bearing a somewhat ragged membranous fringe along the outer edge and resembling reduced epimera (Figs. 43 and 61). The genital segment (Figs. 43 and 44) is greatly widened, 280 μ in length (including the attached spermatophores) $\times$ 325 μ in greatest width. An intersegmental sclerite extends ventrally and laterally between the segment of leg 5 and the genital segment. The egg sacs are attached far forward and laterally on the genital segment, lying dorsally to the fifth legs. Each egg sac is moderately elongated (Fig. 41), about 430 $\times$ 154 μ, and contains many small eggs.

The spermatophores are cemented firmly to the posterolateral areas of the genital segment in all females observed (Figs. 43 and 44).

The three postgenital segments measure 75, 53, and 41 μ in length, respectively. The surfaces of these segments (and the genital segment) show a few hairs and refractile points, as indicated in the figures. The last postgenital segment has dorsally a flap-like operculum (Fig. 45) extending into the wide anal area. The sides of the aperture are finely rugose so as to produce the appearance of striations around the operculum. The last segment bears a short row of very small spinules on its ventral posterior margin near the insertion of each ramus.

The caudal ramus (Fig. 45) is inserted somewhat ventrally, and measures 71 $\times$ 20 μ, about 3.6 times longer than wide, the length being taken along the inner edge. A small hyaline hair (setule ?) is situated on the outer margin near the base. The dorsal seta has lateral hairs. The lateral seta and the outermost terminal seta have minute spiniform projections about midway along their lengths (two such projections on the former and one on the latter), beyond which the setae are annulated. The innermost distal seta is 112 μ in length, with conspicuous lateral hairs along the inner edge and less well-developed hairs along the outer edge. The inner long terminal seta is 414 μ in length, the outer 240 μ, both with short outer spinules and long inner hairs and both showing a basal peg. The distal end of the ramus overlaps ventrally the insertions of the four terminal setae.

The rostral area (Fig. 46) is slightly protuberant anteriorly but weakly developed, with a few hairs as shown in the figure.

The first antenna (Fig. 47) is 7-segmented, about 350 μ in length, the lengths of the segments from the base, respectively, 20, 49, 49, 58, 44, 50, and 38 μ (measured along their non-setiferous margins). The first segment bears 4 setae, the second 15, the third 6, the fourth 3, the fifth 4 and 1 aesthete, the sixth 2 and 1 aesthete, and the seventh 7 and 1 aesthete; the formula thus

being the same as in *H. axiophilus*. The aesthetes on segments 5 and 6 have their basal portions (about one-fifth) sclerotized like a seta. All the long setae are annulated and naked. The longest seta on the last segment is unusually long, about 290 μ.

The second antenna (Fig. 48) is 4-segmented, with the third segment considerably produced on the inner (anterior) corner and bearing four elements: two of them relatively short spines with a flange of spinules on the anterior side and a subterminal setule, the third very long and strongly recurved with annulations and a spinulose flange (Fig. 49), and the fourth a naked annulated seta. The fourth segment is subcylindrical, 40 × 20 μ, and bears 7 setae, of which the outermost has distinct lateral hairs and is relatively short; the remaining 6 setae are either naked or show very short lateral spinules as indicated in the figure.

The labrum (Fig. 50) is slightly trilobed, with teeth and setules as shown in the figure. The two metastomal areas have a complex ornamentation, as indicated in Figure 50.

The mandible (Figs. 51 and 52) is provided terminally with two stout elements of unusual shape for the genus, both of them edged with tooth-like serrations (perhaps modified spines ?) and the outer one having a dorsal protuberance that fits into a concavity on the adjacent element, and with two inner spinulose spines. The paragnath (Figs. 50 and 53) is an elongated hairy lobe. The first maxilla (Fig. 54) is similar to that of other species. The second maxilla (Fig. 55) has the same armature as in that of other species, but the ornamentation of the spines and setae is less strongly developed, and the accessory spinous processes of the terminal compound element are replaced by spinulose flanges. The maxilliped (Fig. 56) is small and rather slender. The bases of the two maxillipeds are connected ventrally by a weak line perhaps representing a trace of the intercoxal plate.

The armature of legs 1–4 (Figs. 57, 58, 59, and 60) has the same formula as in *H.*

axiophilus. The element distal to the two outer spines on the third exopod segment of all four legs is here considered as a modified seta, since it shows annulations. The outer seta on the basis of legs 2 and 3 is relatively short, but in legs 1 and 4 this seta is long, reaching 200 μ in length in leg 4 (longer than the entire exopod which is about 140 μ long).

Leg 5 (Fig. 61) has two segments, the distal one elongate, 110 × 34 μ, or about 3 times longer than wide. There are rows of long spinules on both outer and inner margins. The three spines measure 49, 35, and 54 μ in length, respectively, from outer to inner. The seta is 99 μ long. The seta on the basal segment of the leg is 112 μ in length.

Leg 6 is apparently absent.

In life, in transmitted light, the body is nearly colorless, the eye red, and the spermatophores brownish.

Male.—The body length (not including the setae on the caudal rami) is 1.0 mm (0.92–1.0 mm) and the greatest width is 0.39 mm (0.35–0.41 mm), based on 10 individuals. The form of the body (Fig. 62) is much like that of the female. The ratio of the length of the prosome to that of the urosome is about 1.4 : 1. The segment bearing leg 5 shows dorsally the two raised lobes only weakly developed, and lacks the membrane seen in the female. The genital segment (Fig. 63) is widened, 195 μ in length × 234 μ in greatest width, with its lateral margins more evenly rounded than in the female. The four postgenital segments are 65, 55, 43, and 36 μ in length, respectively. There are scattered hairs and refractile points over the surface of the urosome as shown in the figure.

The caudal ramus resembles that of the female.

The spermatophore while inside the body of the male has the form shown in Figure 63, with its neck arising subterminally on the inner anterior margin. The greatest length of the spermatophore is 130 μ, the width anterior to the neck 78 μ, and the width in the posterior third 49 μ.

The rostral area is like that of the female.

The first antenna is similar to that of the female, but the third and fourth segments have an additional seta (7 and 4, respectively, as in the male of *H. axiophilus*), indicated in Figure 64.

The second antenna resembles that of the female.

The labrum, metastomal areas, mandible, paragnath, and first maxilla are essentially like those of the female.

The second maxilla (Figs. 65 and 66) has the large dorsal spine transformed into a very large, blunt, strongly sclerotized, claw-like process. The compound element is also modified.

The maxilliped (Fig. 67) has a single seta on the first segment. The second segment has its proximal inner angle greatly expanded, with the inner margin of the segment being distinctly curved (not almost straight as in *H. axiophilus*). The length of this segment is 150 μ along the outer edge and its greatest width is 117 μ. Along its inner surface there are two rows of stout spines and a row of slender spinules, plus the usual two small setae. The third segment is very short and unarmed. The fourth segment forms part of the long claw which is 179 μ in length (measured along its axis and not along the curvature). The claw has an interrupted membranous fringe along part of its concave edge, and near its base bears two small setae (the one on the anterior surface of the claw annulate) and a spinous process, as shown in the figure. A distinct transverse line may be seen ventrally between the bases of the maxillipeds (Fig. 68), probably representing the edge of the intercoxal plate.

Leg 1 lacks the inner spine on the basis (Fig. 69); otherwise legs 1–4 are similar to those of the female, with the same spine and setal formula but with somewhat larger endopod spines.

Leg 5 (Fig. 70) has a single free segment which is shorter than in the female, measuring 99 × 43 μ, or about 2.3 times longer than wide. Its armature resembles that of the female (the three spines being 53, 47,

and 53 μ in length, respectively, from outer to inner, and the seta 66 μ). The seta on the basal area is shorter than in the female (about 60 μ in length).

Leg 6 (Figs. 71 and 72) consists of a ventrolateral posterior flap bearing a spine 47 μ in length with fine lateral spinules.

The color in life resembles that of the female.

Remarks on its biology.—Each time that *H. amplicaudatus* was collected it was found in company with *H. axiophilus*, though in smaller numbers. As in the case of *H. axiophilus*, this species seems to show a preference for *Axius* burrows, apparently living in the water rather than on the bodies of the crustaceans, since no copepods were recovered after washing the bodies of *Axius*.

Relationship to other species.—*H. amplicaudatus* differs in its unusually broad genital segment from all known species of *Hemicyclops* that have four setae on the first segment of the first antenna. Only one species, *H. aberdonensis* (T. and A. Scott, 1892), shows a genital segment approaching that of *H. amplicaudatus* in width, but here the shape is very different (see the Scotts' pl. VI, figs. 1 and 12). Other distinctive features are the form of the spermatophores, the unusually long, recurved, fringed spine on the third segment of the second antenna, and the unusual shape of the two stout elements on the end of the mandible.

Hemicyclops carinifer[1] n. sp.

Pl. XI, figs. 73–81; Pls. XII–XV; Pl. XVI, figs. 109–115

Type material.—16 females and 4 males from water in burrows 3–4 cm in diameter and more than 90 cm deep, of unknown origin, in intertidal sand at Bamoko, 3 kilometers north of Dzamandzar, Nosy Bé, Madagascar. Collected by A. G. Humes October 22, 1960. Holotype female, allotype, and 11 paratypes (10 females and 1

[1] The specific name *carinifer*, from Latin *carina* = a keel, and *ferre* = to bear, alludes to the keel-like ridge on the ventral area between the maxillipeds and the first pair of legs.

male) deposited in the United States National Museum, Washington; 6 paratypes (5 females and 1 male) in the Museum of Comparative Zoology, Cambridge, Mass.; and one dissected paratype male in the author's collection.

Other specimens (from similar burrows). —19 females in sand near the village of Antafiabe, on the western shore of Nosy Faly, an island to the east of Nosy Bé, October 21, 1960; 1 female in sand on the southeastern shore of Nosy Sakatia, opposite the village of Antanambe, about 3 kilometers west of Nosy Bé, October 23, 1960; 16 females, 11 males, and 1 copepodid in muddy sand at the Centre d'Océanographie et des Pêches, Pointe à la Fièvre, Nosy Bé, August 28, 1960; 2 females from the same locality, August 22, 1960; 1 female in muddy sand near mangroves at Ambanoro, across the bay from the Centre d'Océanographie et des Pêches, Nosy Bé, August 23, 1960; 36 females, 9 males, and 1 copepodid from sand west of Pte. Ambarionaomby, Nosy Komba, March 14, 1964; 10 females from the same locality, March 28, 1964; 21 females and 5 males in sand at Bamoko, Nosy Bé, February 29, 1964; 2 females and 1 male from sand at Antviabe, on the southern shore of Nosy Komba, March 16, 1964; 6 females from sand at Nosy Kisimany, 25 kilometers southwest of Nosy Bé, April 12, 1964; 2 females from sand at Madirokely, Nosy Bé, April 28, 1964; 12 females and 2 males from sand at Befotaka, Nosy Bé, April 29, 1964; 22 females and 12 males from sand at Nosy Roty, near Nosy Sakatia, May 12, 1964; 6 females and 2 males from muddy sand at Ampassipohe, Nosy Bé, May 11, 1964; and 1 female from sand at Boloboxo, Nosy Faly, May 13, 1964.

Female.—The length of the body (excluding the setae on the caudal rami) is 1.42 mm (1.32–1.55 mm), and the greatest width (in the posterior half of the cephalosome) is 0.50 mm (0.45–0.52 mm), based on 10 individuals. The body (Fig. 73) has a rather slender form, the prosome being only slightly longer than the urosome, with the ratio 1.18 : 1. The dorsal body surface

has relatively few small hairs. The epimera are prominent but have subacute or rounded posterolateral angles in dorsal or ventral view. The genital segment (Fig. 74) is wider than long, 132×161 μ, broadest in its anterior third, and with the median posterior dorsal surface raised and abruptly truncated (Fig. 75), forming a transverse crescentic sclerotized line in dorsal view. The egg sacs are attached dorsolaterally near the widest part of the segment. Near the attachment of each egg sac there are three slender naked setae (Fig. 76), 62, 57, and 23 μ in length, respectively, borne within the genital area surrounding the oviducal opening. Each sac is slender and elongated, 560×123 μ, held parallel to the abdomen in preserved specimens, and containing 4 rows of approximately 12 eggs each (Fig. 77).

No spermatophore was found attached to the female.

The four postgenital segments measure 91, 78, 55, and 117 μ in length, respectively. The anal segment (Figs. 78 and 79) has a posterior fringe of small spinules extending from each side dorsally and ventrally near the insertions of the rami; this segment shows dorsally a large, oval, weakly sclerotized anal region and ventrally a pair of transverse rows of slender spinules near the anterior edge.

The caudal ramus (Fig. 80) measures 220×27 μ (the width taken at its midregion, the length along its inner edge), about 8.0 times longer than wide. A small hyaline hair (setule ?) is situated on the outer margin in the proximal third. The lateral seta is naked, 49 μ in length. The dorsal seta, borne on a minute basal segment, is naked, 122 μ long. The outermost terminal seta is naked, 59 μ long. Of the 2 long terminal setae, the outer one is 426 μ and the inner one 280 μ in length, both with a basal peg and with lateral hairs. The innermost terminal seta is 114 μ in length and haired along its inner edge. The distal end of the ramus slightly overlaps ventrally the insertions of the 4 terminal setae.

The rostral area (Fig. 81) is small and inconspicuous, set off from the anterior surface of the head by a furrow, and protruding ventrally.

The first antenna (Fig. 82) is about 582 μ in length, with 7 segments, in length from the base, 55, 91, 33, 130, 83, 83, and 106 μ (measured along their forward setiferous margins). The first segment bears 5 setae, the second 15, the third 6, the fourth 3, the fifth 4, the sixth 2 and 1 aesthete, and the seventh 7 and 1 aesthete. Certain of the setae have lateral hairs, as indicated in the figure. The terminal aesthete seems to insert independently of any seta.

The second antenna (Fig. 83) is 4-segmented, with the third segment not produced on the inner distal corner and bearing there 4 setae as indicated, the largest similar in structure to the 4 terminal curved setae; the last segment is slender and elongated, 105 × 22 μ, about 4.8 times longer than wide, with the usual 7 elements. The long spinules along the edges of the third and fourth segments are rather flattened and have brush-like tips (as in Fig. 84).

The labrum (Fig. 85) has the usual transversely oval shape, its free margin having a row of large teeth, its sublateral areas a few spinules, and its lateral areas groups of hairs.

The metastomal areas (Fig. 86) have an ornamentation as shown in the figure.

The mandible (Fig. 87) has a terminal armature consisting of a stout spine with teeth on each side, two more slender lamelliform spines bearing lateral spinules, and a very small spinule. The paragnath (Fig. 88; see also Fig. 86) is a lobe bearing a distal row of teeth (broad spinules ?), a small semicircular subapical lobe, and two groups of hairs on its posterior surface which merge into a proximal patch; the more ventral row of these hairs continues distally into a line of minute denticles. The first maxilla (Fig. 89) and the second maxilla (Fig. 90) have the number and arrangement of the spines and setae similar

to other species, but with minor differences in their lateral spinules as indicated in the figures. The maxilliped (Fig. 91) has a large inner process on the fourth segment, this process being distinctly bent, approaching an S in contour; there are 2 slender setae arising from the terminal segment; the tips of the S-shaped process and of the terminal element are rather blunt, while the proximal seta on the first segment and the 2 setae on the second segment have minutely bifid tips (see Fig. 92). The bases of the maxillipeds are connected ventrally by a cuticular line (Fig. 93) probably representing a trace of the intercoxal plate.

The area between the bases of the maxillipeds and the first pair of legs, forming the postoral protuberance, lacks ornamentation but shows prominent lateral sclerites (Fig. 93), and is produced medially to form a longitudinal keel (Fig. 94).

The armature of legs 1–4 (Figs. 95, 96, 97, and 98) is as follows:

P1	protopod	0:1	1:1	exp	I:0	I:1	III,5
				end	0:1	0:1	I,5
P2	protopod	0:1	1:0	exp	I:0	I:1	III,6
				end	0:1	0:2	I,II,3
P3	protopod	0:1	1:0	exp	I:0	I:1	I,II,5
				end	0:1	0:2	I,III,2
P4	protopod	0:0	1:0	exp	I:0	I:1	I,II,5
				end	0:1	0:1	I,III

Leg 1 bears on the basis a straight inner spine 50 μ in length; the outer distal corner of the second endopod segment of this leg forms a spiniform process. Leg 4 shows the rami relatively more elongated than in the preceding legs; the last endopod segment has four spines, 31, 52, 87, and 26 μ in length from outer to inner, respectively. The coxa of leg 4 lacks an inner seta. All four legs show minute flagella near the tips of the outer exopod spines. Legs 1–3 show 2–3 unusually strong lateral spinules on the outer side of the bases of certain of the distal setae on the last endopod segment, as shown in the figures.

Leg 5 (Fig. 99) has a ventral row of spinules near the seta on the basal segment. The distal segment is elongated, 114 μ

along its inner edge; it is wider in its basal half (45 μ) than in its distal half (36 μ), and deeply indented at the insertion of the lateral seta. There is an outer marginal row of spinules on the basal half, and a similar inner row of spinules along part of the margin of the distal half. The outer margin forms a blunt projection near the insertion of the marginal spine and also near the distal outer spine; there is a row of slender spinules ventrally on these projections. There is also a row of minute spinules ventrally near the insertion of the inner distal spine. The 3 spines and the seta measure 42, 42, 77, and 49 μ in length from outer to inner, respectively.

Leg 6 is apparently absent, but may be represented by the 3 setae near the egg sac attachments.

The color in living specimens, in transmitted light, is translucid, slightly amber or reddish brown, with reddish orange globules in the prosome, the ovary dark gray, the eye red, and the egg sacs reddish gray to orange.

Male.—The body length (not including the setae on the caudal rami) is 1.61 mm (1.57–1.66 mm) and the greatest width is 0.55 mm (0.53–0.58 mm), based on 4 individuals. The ratio of the prosome to urosome is 1.35 : 1, with the prosome only slightly longer (Fig. 100) than in the female. The genital segment (Fig. 101) is nearly quadrate in dorsal or ventral view, measuring 156 × 151 μ. The 4 postgenital segments have proportions similar to those of the female. The ornamentation of the anal segment is also like that in the female.

The caudal ramus is as in the female.

Spermatophores were seen only inside the genital segment of the male (Fig. 101).

The rostral area resembles that of the female.

The first antenna is similar to that of the female, but the third segment has 7 setae and the fourth 4 setae (see Fig. 102).

The second antenna is like that of the female.

The labrum (Fig. 103) has a row of slender spines along its free edge and a row of additional, broad, scale-like denticles curving dorsally along the posteroventral face on either side. The metastomal areas are much like those of the female, but the most posterior rows of spines are smaller (Fig. 104).

The mandible, paragnath, first maxilla, and second maxilla are similar to those of the female.

The maxilliped (Figs. 105 and 106) has 2 unequal setae on the first segment, the proximal seta with prominent lateral spinules, the distal one naked. The second segment is slender, 239 × 101 μ, with 2 rows of broad spinules and 2 annulated setae on its inner surface; one of these rows is interrupted by the bases of the setae, proximal to which the row becomes a series of blunt serrations and then a group of broad spinules. The third segment is short and unarmed. The fourth segment forms part of the claw, which is 260 μ in length (measured along its axis and not along the curvature), slightly sinuous in outline, and with a distinct flexure near its tip, where there is a small outer lamella and 2 rows of denticle-like ridges which decrease in size proximally. Near the base of the claw there may be seen a setiform process and 3 slender setae (the one nearest to the process recurved and unilaterally haired) (see Fig. 107).

The postoral area between the bases of the maxillipeds and the first pair of legs (Fig. 108) is raised to form a ventral longitudinal keel (Fig. 109). This keel bears a row of serrations along its edge, a short transverse crescentic row of irregular serrations anteriorly, and laterally a few minute refractile points. Between the bases of the second maxillae there is a minute bifurcated sclerotization.

Legs 1–4 have the same number and arrangement of spines and setae as in the female. The inner spine on the basis of leg 1 (Fig. 110) is larger than in the female and slightly recurved, about 77 μ in length, with a transverse weakening in the sclerotization in its basal third, a row of minute refractile points, and a cluster of rather

blunt minute spinules near its tip (Fig. 111). The second endopod segment of leg 1 does not show a distal outer spiniform process as in the female. The middle spine on the outer side of the third exopod segment of leg 1 is relatively smaller than in the female. Leg 2 shows the 3 spines on the third endopod segment of different proportions than those of the female, their lengths from outer to inner being 38, 28, and 77 μ, the middle spine being distinctly shorter and more slender (Fig. 112). There is on this endopod only a single terminal spiniform process. (One male showed the distal margin of the third endopod segments of leg 3 with a single spiniform process between the 2 middle spines on one leg, and with a bifurcated process at this point on the opposite leg, as indicated in Fig. 113).

Leg 5 (Fig. 114) is similar to that of the female, but the row of spinules on the distal inner margin of the distal segment is shorter, and the processes near the bases of the 2 outermost spines are more acute than rounded.

Leg 6 (Fig. 115) consists of a small ventrolateral flap on whose extreme lateral portion a slender seta 34 μ in length is borne on a slight prominence.

The color in living specimens resembles that of the female.

Remarks on its biology.—*H. carinifer* frequently occurred in the same burrows with the following species (in 10 of 16 collections).

Relationship to other species. — This copepod falls in the group of *Hemicyclops* species having five setae on the first segment of the first antenna, an elongated terminal segment on the second antenna, and elongated caudal rami. Four species attributable to this group (*H. elongatus* Wilson, 1937, *H. adhaerens* (Williams, 1907), *H. subadhaerens* Gooding, 1960, and *H. arenicolae* Gooding, 1960) have in the female a caudal ramus which is much shorter than in *H. carinifer* (only a little more than 4 times longer than wide, or less). These species also appear (as nearly as can be as-

certained from the published descriptions) to lack two features of *H. carinifer*, namely, the projections near the insertions of the two outer spines on the distal segment of leg 5, and the keel on the ventral surface between the maxillipeds and the first legs.

Hemicyclops diremptus[1] n. sp.

Pl. XVI, figs. 116–117; Pls. XVII–XX; Pl. XXI, figs. 147–152

Type material.—6 females and 5 males from burrows of unknown origin 3–4 cm in diameter and more than 90 cm deep in intertidal sand near the village of Antafiabe, on the western shore of Nosy Faly, an island to the east of Nosy Bé, Madagascar. Collected by A. G. Humes October 21, 1960. Holotype female, allotype, and 3 paratypes (2 females and 1 male) deposited in the United States National Museum, Washington; 2 paratypes (1 female and 1 male) in the Museum of Comparative Zoology, Cambridge, Mass.; and the remaining paratypes in the author's collection.

Other specimens (from similar burrows). —1 male from sandy mud in front of the Centre d'Océanographie et des Pêches, Nosy Bé, August 22, 1960; 8 females in sand west of Pte. Ambarionaomby, Nosy Komba, March 14, 1964; 2 females from the same locality, March 28, 1964; 1 male from sand north of Antafiabe, Nosy Faly, March 15, 1964; 5 females and 13 males from sand at Nosy Kisimany, April 12, 1964; 1 female and 2 males from sand at Madirokely, Nosy Bé, April 28, 1964; 176 females and 118 males from sand at Befotaka, Nosy Bé, April 29, 1964; 77 females and 21 males from sand at Nosy Roty, near Nosy Sakatia, May 12, 1964; 15 females and 22 males from muddy sand at Ampassipohe, Nosy Bé, May 11, 1964; and 1 female and 2 males from sand at Boloboxo, Nosy Faly, May 13, 1964.

Female.—The length of the body (not including the setae on the caudal rami) is

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[1] The specific name *diremptus*, from Latin *dirempere* = to separate, divide, alludes to the divided condition of the genital segment in the female.

1.90 mm (1.82–1.97 mm), and the greatest width (in the posterior part of the cephalosome) is 0.81 mm (0.76–0.87 mm), based on 6 individuals. The prosome is moderately broad and a little longer than the urosome, the ratio being about 1.37 : 1 (Fig. 116). In dorsal or ventral view the epimera are conspicuous and angulate. The segment bearing leg 5 is narrow in front and broadened posteriorly at the level of the legs, where it shows a dorsal transverse sclerotized ridge (probably a remnant of the epimeron of this segment). An intersegmental sclerite occurs between the first two urosomal segments. The genital segment (Figs. 117, 118, and 119) is widened and divided transversely into an anterior portion bearing the attachments of the egg sacs and a slightly narrower posterior portion. The length of the genital segment is 195 μ, the anterior part being 117 $\times$ 273 μ and the posterior part 78 $\times$ 229 μ.

The egg sacs are attached dorsolaterally on the anterior half of the genital segment between small dorsolateral and more extensive ventrolateral flanges (see Fig. 119). Each egg sac is about 560 $\times$ 200 μ, and contains numerous small eggs (Figs. 116 and 117).

The three postgenital segments measure respectively 114 $\times$ 178 μ, 62 $\times$ 133 μ, and 62 $\times$ 114 μ, the first segment being longer, wider, and more globose than the other two, which are somewhat more closely associated. The last segment has near the insertion of each caudal ramus a ventral transverse row of about four small spinules followed by a row of much smaller spinules (see Figs. 119, 120, and 121). The thinly sclerotized anal area occupies virtually the whole dorsal side of the anal segment. There is no anal plate, but the posterior edge of the preceding postgenital segment is modified (see Fig. 121).

The dorsal surface of the prosome and the dorsal and ventral surfaces of the urosome are covered with minute hairs, each arising from a refractile point.

The caudal ramus (Fig. 121) is elongated,

117 $\times$ 24 μ (the length measured along the inner edge and the width at the middle of the ramus), nearly 5 times longer than wide. A small hyaline hair occurs on the basal outer margin and a few minute hairs are to be found on the ventral surface. The lateral seta is 47 μ in length and the outermost terminal seta is 65 μ, including the basal shaft and the distal flagelliform part. The dorsal seta is 91 μ long and bears only a few lateral hairs. The innermost terminal seta is 112 μ in length with an inner row of hairs. The inner long terminal seta is 728 μ and the outer one 437 μ in length, both with lateral spinules, these being at first widely spaced and long, then in the distal two-thirds of the setae short and closely spaced.

The rostral area (Fig. 122) is very weakly developed.

The first antenna (Fig. 123) is about 400 μ long, 7-segmented, the segments, beginning at the base, 20, 55, 52, 88, 51, 55, and 47 μ in length (measured along their non-setiferous margins). The formula for the armature is 4, 15, 6, 3, 4 + 1 aesthete, 2 + 1 aesthete, and 7 + 1 aesthete. Most of the setae are annulated with minute lateral hairs, but there are a few setae which are entire with longer lateral hairs (1 on the second segment, 2 on the fifth, 1 on the sixth, and 4 on the seventh).

The second antenna (Fig. 124) is 4-segmented, with the third segment produced on the inner distal corner where it bears four elements: proximally a small posterior seta, more distally a large and slightly sinuous spine, and distally two more slender and somewhat recurved spines with subterminal setules. The fourth segment is quadrate in flat view, 29 $\times$ 29 μ, and bears seven setae, the four long curved setae with their tips not as attenuated as the others, and the outermost of these seven setae lying across the bases of the others and having long lateral spinules.

The labrum (Fig. 125) is tilted forward, so that the ventral view shown in the figure is equivalent to posterior in other species.

The labrum is somewhat trilobed and has setules and teeth as shown in the figure; there is a curved row of long hyaline setules along the anteroventral margin. The metastomal areas have a complex ornamentation, as indicated in Figure 125.

The mandible (Fig. 126) has the usual two stout elements and two well-developed setae with lateral hairs. The paragnath (Figs. 125 and 127) is a stout hairy lobe. The first maxilla (Fig. 128) is similar in structure to that of other species; it has prominent lateral spinules on certain of the setae. The second maxilla (Fig. 129) is armed as in other species, the innermost spine on the second segment having long outer spinules. The maxilliped (Fig. 130) shows the two setae on the second segment with prominent lateral spinules, and the margin distal to these two setae bears a row of hairs. The last maxilliped segment (Fig. 131) bears two large setae (spines?) (one of them with about five very long slender spinules on its inner margin), four more slender setae, and a row of 4–5 slender hyaline setules on the outer side near the bases of the spines. The bases of the maxillipeds are connected by a ventral transverse line as indicated in Figure 125.

The postoral protuberance is poorly differentiated.

The armature of legs 1–4 (Figs. 132, 133, 134, and 135) is similar to that of *H. axiophilus* and *H. amplicaudatus*, although certain elements are difficult to classify as a "spine" or a "seta." In leg 1 the inner spine on the basis is 65 μ in length, its inner margin serrated and its outer margin with a row of short hairs; the margin of the basis medial to this spine is prominently rounded and smooth. In legs 2–4 this inner area of the basis has a broadly rounded margin and bears a row of short marginal setules and another row of hyaline spinules on its anterior surface. The ventral margin of the intercoxal plate of leg 1 bears on each side a row of hairs; in legs 2–4 this margin has on each side a patch of long spinules. The

outer margin of the coxa of leg 4 lacks the long hairs seen in the preceding three legs.

Leg 5 (Fig. 136) has a rather broad and short free segment (its greatest diagonal length from the outer proximal corner to the inner distal angle 143 μ, its length along the inner side 125 μ, its greatest width 105 μ). There are rows of spinules on the distal half of both the outer and inner margins. The three spines are 48, 63, and 50 μ in length, respectively, from outer to inner; the seta is very short, only 34 μ in length. A row of spinules occurs laterally on the basal area of the leg just anterior to the insertion of the free segment. The seta on the basal area is 68 μ long. Traces of a basal segment may be seen in the pattern of sclerotization on the segment of leg 5; the fifth legs are joined ventrally by a strong ridge near the posterior edge of this segment.

Leg 6 is apparently absent.

The color in living specimens, in transmitted light, is translucid, the eye red.

Male.—The length of the body (not including the setae on the caudal rami) is 1.14 mm (1.04–1.28 mm) and the width in the posterior part of the cephalosome is 0.48 mm (0.44–0.52 mm), based on 4 individuals. The ratio of the length of the prosome to that of the urosome is about 1.36 : 1 (Fig. 137). The epimera are prominent as in the female. The genital segment (Fig. 138) is undivided and subcircular in dorsal or ventral view, 143 μ long × 174 μ wide. The spermatophore (seen only within the body of the male) is elongated (Fig. 139), 99 × 36 μ including the neck of 13 μ.

The four postgenital segments are respectively 68, 60, 40, and 40 μ in length.

There are hairs and refractile points on both the urosome and prosome as in the female, but the general sclerotization seems to be stronger.

The caudal ramus (Fig. 140) is shorter than in the female, 55 μ (the length along the inner edge) × 28 μ (the greatest width), or two times longer than wide. The setae are arranged as in the female.

The rostral area (Fig. 141) is a little better defined than in the female.

The first antenna is similar to that of the female, but the third segment has 7 setae and the fourth 4 setae (Fig. 142). The second antenna is like that of the female.

The labrum and the metastomal areas (Fig. 143) are generally like those of the female, but the long hyaline setules on the anteroventral margin of the labrum are absent, and the second metastomal area shows only a single row of broad tooth-like spines.

The mandible, paragnath, and first maxilla are like those of the female. The second maxilla (Fig. 144) is similar to that of the female, but the spinules on the innermost spine of the second segment are much less developed.

The maxilliped (Figs. 145 and 146) has a single long seta on the first segment. The second segment has its proximal inner angle greatly expanded, making the segment almost pyriform in outline. The length of this segment along the outer margin is 114 μ, its greatest length along the inner spinose margin is 143 μ, and the greatest width is 112 μ. There are three rows of stout, rather blunt spines along the inner margin, in addition to the usual two setae. The third segment is very short and unarmed. The fourth segment forms part of a long claw 148 μ in length (measured along its axis and not along the curvature), bearing near its base a small seta on the posterior side, and a spinous process and a minute setule on the inner curvature. The transverse line on the ventral surface between the bases of the maxillipeds is weakly developed.

Leg 1 lacks the inner spine on the basis (Fig. 147). Otherwise the spine and setal formula of legs 1–4 is like that of the female. There is a slight sexual dimorphism in the last endopod segment of legs 2–4 (Figs. 148, 149, and 150), where the terminal spine-like processes are reduced and the sclerotization at the base of the two distal spines is stronger.

Leg 5 (Fig. 151) has a free segment which is not as broad as in the female, measuring 85 μ long (along the inner side) $\times$ 51 μ in greatest width. Its armature is like that of the female.

Leg 6 (Fig. 152) consists of a ventral flap on the posterior part of the genital segment. It bears a stout spine 30 μ long with minute lateral spinules.

The color is like that of the female.

Remarks on its biology.—*H. diremptus* was often found in burrows along with *H. carinifer* (in 10 of 11 collections).

Relationship to other species.—*H. diremptus* belongs to the group of species with four setae on the basal segment of the first antenna, along with *H. axiophilus* and *H. amplicaudatus.* It differs from all other species in this group in having a distinctly divided genital segment in the female. In the original description of *H. bacescui* (Şerban, 1956) the genital segment is described as double, and Stock (1959), who has restudied the species, mentions a trace of a suture on its dorsal surface. The division is much weaker, however, than in *H. diremptus. H. bacescui* further differs from the new species in the form of the fifth legs and the caudal rami. *H. indicus* Sewell, 1949, shows lateral indentations on the female genital segment (see Sewell's fig. 16A), but the segment is single. Although this species shows certain similarities to *H. diremptus* (for example, in the form of the fifth legs and in the armature of the second maxilla), it differs in the form of the caudal ramus, in the relative length of the second and third segments of the first antenna, and in the size of the body. The female of *H. leggii* (Thompson and Scott, 1903) is unknown, but the male differs from that of the new species in its body length, in the relative lengths of the first antennal segments, in the form of the innermost terminal spine on the second segment of the second maxilla, in the shape of the second segment of the maxilliped, and in the size of the caudal ramus. The fifth leg of *H. leggii* seems to resemble closely that of the new species.

Hemicyclops kombensis[1] n. sp.

Pl. XXI, figs. 153–154; Pls. XXII–XXVI

Type material.—3 females and 2 males from water in burrows of unknown origin 3–4 cm in diameter and more than 90 cm deep in intertidal sand west of Pte. Ambarionaomby, Nosy Komba, near Nosy Bé, Madagascar. Collected by A. G. Humes March 14, 1964. Holotype female, allotype, and one paratype female deposited in the United States National Museum, Washington; the remaining female and male dissected and in the collection of the author.

Other specimens (from similar burrows). —1 male from sand in front of the village of Antviabe, on the southern shore of Nosy Komba, March 16, 1964; 1 female and 1 male from sand at Madirokely, Nosy Bé, April 28, 1964; and 1 female from sand at Nosy Roty, near Nosy Sakatia, May 12, 1964.

Female.—The length of the body (not including the setae on the caudal rami) is 2.27 mm (2.26–2.29 mm), and the greatest width is 0.83 mm (0.80–0.89 mm), based on 3 individuals. The prosome is moderately broad and only slightly longer than the urosome, the ratio being about 1.08 : 1 (Fig. 153). In dorsal or ventral view the epimera of the segments of legs 1–4 are conspicuous and angulate. The segment of the fifth legs shows a dorsal transverse sclerotized band, bearing a row of long slender spinules on each side (Fig. 154). An intersegmental sclerite, best seen from the ventral side, occurs between the first two segments of the urosome. The genital segment (Figs. 154 and 155) is elongated, with the sides nearly parallel except for slight swellings near the attachments of the egg sacs, and shows dorsally in the middle of the segment a transverse internal sclerotization. The segment measures 475 μ in length; its width in the anterior one-fourth is 305 μ and in the posterior half 271 μ.

The egg sacs are attached ventrolaterally far forward on the genital segment, between small dorsal and ventral flanges (Fig. 155). Near the point of attachment there are two minute, rather obscure spiniform processes, each about 10 μ in length. Each egg sac is elongated oval, 633 × 249 μ, and contains numerous rather small eggs (Fig. 156).

The three postgenital segments measure, respectively, 203 × 220, 140 × 184, and 92 × 158 μ. The last segment is thus shorter and narrower than the preceding ones; there is no apparent anal operculum. Above and below the insertion of each caudal ramus there are slight flanges, the dorsal one smooth, the ventral one with an outer row of minute spinules and an inner row of larger spinules (Fig. 157).

The dorsal surface of the prosome and the dorsal and ventral surfaces of the urosome bear minute hairs and refractile points.

The caudal ramus (Fig. 157) is moderately elongated, 170 μ in length, 70 μ wide near the base, 62 μ at the middle, and 54 μ near the distal end; taking the width at the middle, the ramus is 2.74 times longer than wide. A small hyaline hair arises from the outer basal margin. The lateral seta is 68 μ in length and shows only a slight differentiation into a basal shaft and a distal flagellum. The outermost terminal seta is 117 μ long, including the basal shaft of 68 μ and the distal flagelliform part of 49 μ. The dorsal seta is 149 μ long and bears a few lateral hairs. The innermost terminal seta is 260 μ in length and bears lateral spinules, those along the inner side being longer and better developed. The inner long terminal seta is 948 μ and the outer one 588 μ in length, the middle region of both bearing short outer spinules and longer inner hairs (see Fig. 153). The four terminal setae are inserted somewhat dorsally and the resulting ventral flange at the end of the ramus bears a row of minute spinules and a group of longer spinules on the inner angle. Along the distal third of the inner margin of the ramus there is a row of long slender spinules.

[1] The specific name *kombensis*, a combination made from Nosy Komba and Latin *-ensis* = living in, refers to the island where this species was first found.

The rostral area (Fig. 158) is moderately well defined.

The first antenna (Fig. 159) is about 510 μ long, 7-segmented, the segments, beginning at the base, 15, 74, 65, 110, 65, 73, and 56 μ in length (measured along their non-setiferous margins). The formula for the armature is 4, 15, 6, 3, 4 + 1 aesthete, 2 + 1 aesthete, and 7 + 1 aesthete. Most of the setae are annulated and a few of those on the second segment show minute lateral hairs. There are, however, certain entire setae with long lateral hairs (one on the second segment, one on the fourth, 2 on the fifth, one on the sixth, and 4 on the seventh). The armature is thus very similar to that in *H. diremptus*. On the distal anteroventral surface of the second segment there are a few transverse narrow refractile bars.

The second antenna (Fig. 160) is 4-segmented, with the third segment produced on the inner distal corner where it bears four elements: proximally a slender posterior seta, more distally a larger recurved annulated seta, and distally two slender spines bearing unilateral spinules and subterminal setules. The fourth segment is nearly quadrate in flat view, 35 μ in length × 30 μ, and bears seven setae, the four long recurved annulated setae with their tips less attenuated than the others, and the seta lying posteriorly across the bases of the long setae having conspicuous lateral spinules (Fig. 161).

The labrum (Fig. 162) is tilted forward as in *H. diremptus*, and in a ventral and somewhat posterior view has a rather trilobed appearance, with setules and teeth as shown in the figure. The metastomal areas have a complex ornamentation, as indicated in Figure 163.

The mandible (Fig. 164) has two stout elements and two well-developed setae with lateral hairs. The paragnath (Fig. 165) is a moderately elongated lobe bearing hairs and a row of delicate hyaline spinules as indicated. The first maxilla (Fig. 166) is similar in structure to that of *H. diremptus*; the lateral setules on the outermost seta, however, are longer than in that species.

The second maxilla (Fig. 167) is in major respects similar to that of *H. diremptus*. The maxilliped (Fig. 168) has the same general form as in *H. diremptus*, but the two setae on the first segment are more slender, and the two setae on the second segment are relatively shorter; the last segment bears two large recurved setae (spines ?), one of them with conspicuous lateral spinules (four on one side and three on the other), and four slender setae. Between the bases of the maxillipeds there is a ventral transverse line as shown in Figure 169.

The area between the maxillipeds and the first pair of legs shows little differentiation.

The armature of legs 1–4 (Figs. 170–173) is similar to that of *H. axiophilus*, *H. amplicaudatus*, and *H. diremptus*, but again certain elements are difficult to classify as a "spine" or a "seta." In leg 1 the inner spine on the basis is 97 μ in length, with both margins bearing a narrow, finely serrated fringe. The margin of the basis medial to this spine is rounded and smooth except for a small tooth-like process near the base of the spine. In legs 2–4 this inner area of the basis bears a row of slender marginal spinules and another row of larger hyaline spinules on its anterior surface. The ventral margin of the intercoxal plate of leg 1 bears on each side a row of long hairs, but in legs 2–4 these hairs are replaced by rather stout spinules. The outer margin of the coxa of leg 4 lacks the long spinules seen on legs 1–3, but a row of slender spinules occurs on the outer posterior margin. On the last segment of the endopod of leg 4 the two inner elements are setiform, with long lateral hairs basally and short lateral spinules in the distal two-thirds.

Leg 5 (Fig. 174) has a free segment which is shaped rather like a petal, narrow at the base but broadened distally; its greatest length is 180 μ, its greatest width 98 μ, and its width basally 32 μ. There are rows of spinules on both outer and inner margins, those on the outer margin being longer than the others. The three spines are 65, 52, and 71 μ in length, respectively, from outer

to inner; the seta is 89 μ long. Rows of small spinules occur ventrally near the insertions of the three spines. The two outer spines are bilaterally fringed, but the inner spine is fringed outwardly and bears small spinules inwardly. The basal area of leg 5 shows a pattern of sclerotization which suggests a discrete segment; the seta is 110 μ long and lightly plumose distally. There is a row of small spinules adjacent to the seta.

Leg 6 is apparently absent.

The color in living specimens in transmitted light is somewhat opaque to light amber, with reddish globules in the prosome, the eye red, the egg sacs reddish brown.

Male.—The length of the body (without the setae on the caudal rami) is 2.09 mm (1.99–2.19 mm) and the greatest width is 0.77 mm, based on 2 individuals. The ratio of the length of the prosome to that of the urosome (Fig. 175) is about the same as that in the female. The epimera of the segment bearing leg 4 are less angular than in the female. The genital segment (Fig. 176) measures 240 × 287 μ, being wider than long, constricted anteriorly, with the posterolateral areas pointed. Spermatophores were not seen in any of the males collected.

The four postgenital segments measure, respectively, 221 × 205, 170 × 167, 124 × 148, and 82 × 140 μ.

As in the female, the prosome and the urosome bear hairs and refractile points. The general sclerotization of the body is stronger than in the female (see Fig. 187 below).

The caudal ramus (Fig. 177) is relatively shorter than in the female, 132 μ long, 58 μ wide basally, 54 μ in the middle, and 46 μ distally; thus, taking the middle width, the ramus is about 2.4 times longer than wide. The armature of the ramus is like that of the female.

The rostral area is similar to that in the female.

The first antenna is generally like that of the female, but as in the previous species shows an additional seta on the third and fourth segments, the formula being 4, 15, 7, 4, 4 + 1 aesthete, 2 + 1 aesthete, and 7 + 1 aesthete.

The second antenna is similar to that of the female.

The labrum (Fig. 178) shows certain differences in details of the spinules and teeth. The number of large teeth at either side of the transverse row appears to be somewhat variable (see Figure 179 of these teeth in another male). There are two diagonal lines of very small refractile points (spinules?) on each side of the ventral surface of the labrum. The metastomal areas (Fig. 178) are ornamented as indicated in the figure. (In the specimen from which Figure 178 was drawn, the two groups of tooth-like spines on the left side, indicated by broken lines, were missing and presumably broken off.)

The mandible resembles that of the female, but the teeth on the largest element appear to be more pointed (see Fig. 180). The paragnath (Fig. 181) is similar to that of the female, but has a protuberance on the inner margin, which in the female is regular. The first maxilla (Fig. 182) appears to be shorter and less slender than in the female, and, although the long spines and setae are much like those in the opposite sex, there is an additional row of short spinules on the inner margin. The second maxilla (Fig. 183) shows the stout inner element on the second segment here replaced by a strongly sclerotized, rather blunt, claw-like element lacking an articulation with the segment.

The maxilliped (Fig. 184) has a single long seta on the first segment. The second segment has its proximal inner angle greatly expanded. The length of this segment along the outer margin is 224 μ, its greatest length from the distal end to the tip of the inner expansion is 260 μ, and its greatest width is 189 μ. There are three rows of fairly stout spines along the inner surface, in addition to the usual two setae. The third segment is very short and unarmed. The fourth segment forms part of a long recurved claw 270 μ in length (measured along its axis and not along the curvature), bearing near its

base a small seta on the posterior side, and a spinous process and a minute setule on the inner curvature. The ventral surface between the bases of the maxillipeds (Fig. 185) does not show a transverse line. The region between the maxillipeds and the first pair of legs is unmodified as in the female.

Leg 1 lacks the inner spine on the basis (Fig. 186). Otherwise legs 1–4 have a spine and setal formula like that of the female. The sclerotization of the legs, illustrated in the endopod of leg 4 (Fig. 187), seems to be stronger than in the female. (This may be an individual difference, however, since only one male was dissected.)

Leg 5 (Fig. 188) has a free segment which is not broadened distally as in the female, its greatest dimensions being $173 \times 73 \mu$. Its armature is like that of the female.

Leg 6 (Fig. 189) consists of a ventral flap on the posterior part of the genital segment, bearing a strong spine 51μ in length. In dorsal view the sixth leg is completely hidden except for the tip of the spine.

The color in life is similar to that of the female.

Remarks on its biology.—*H. kombensis* was always found in burrows in company with other species of *Hemicyclops*, once with *H. carinifer* and three times with both *H. diremptus* and *H. carinifer*.

Relationship to other species.—*H. kombensis* is included in the group of species having four setae on the basal segment of the first antenna. It may be compared only with the male of *H. leggii* (Thompson and Scott, 1903), since the female of that species remains unknown. The male of *H. leggii*, however, differs in having nearly quadrate caudal rami and in having two setae on the basal segment of the maxilliped. *H. dilatatus* Shen and Bai, 1956, has a "squarish" genital segment in the female. *H. australis* Nicholls, 1944, has two setae on the basal segment of the male maxilliped and the caudal ramus is almost quadrate. *H. indicus* Sewell, 1949, has a genital segment which is very slightly wider than long and the caudal rami are but little longer than broad. In *H.*

purpureus Boeck, 1873, as figured by Sars (1917), the fifth leg in the female is not markedly expanded distally and the caudal rami are relatively shorter than in *H. kombensis*. *H. thysanotus* Wilson, 1935, shows lateral expansions in the anterior part of the genital segment and the form of the fifth leg is different from that in the species from Madagascar. In *H. aberdonensis* (T. and A. Scott, 1892) the genital segment is much wider than long, and there are two setae on the basal segment of the male maxilliped. In *H. thompsoni* (Canu, 1888) the genital segment, though elongate, is expanded in its extreme anterior part. *H. tamilensis* (Thompson and Scott, 1903) has in the female broad lateral expansions on the genital segment, and short, almost quadrate caudal rami. In the female of *H. bacescui* (Serban, 1956) the caudal rami are two times longer than wide, the inner spine on the basis of leg 1 is strongly denticulated (Stock, 1959), and the lateral margins of the genital segment are not almost parallel as in *H. kombensis*. *H. visendus* Humes, Cressey, and Gooding, 1958, shows in the female a genital segment somewhat resembling that of *H. kombensis* but which has a pair of dorsolateral ridges; the caudal ramus is only 1.7 times longer than wide; the third segment of the second antenna bears spinules and setae of a different form than in the species from Madagascar; and the free segment of the fifth leg is oval rather than petal-like in outline. The inner side of the second segment of the male maxilliped of *H. visendus* is broadly inflated rather than angularly produced as in *H. kombensis*.

Hemicyclops biflagellatus[1] n. sp.

Pls. XXVII–XXXI; Pl. XXXII, figs. 221–222

Type material.—24 females and 6 males from water in burrows of unknown origin 3–4 cm in diameter and about 50 cm deep in intertidal muddy sand at Ampassipohe, on the southern shore of the bay of Ambato-

[1] The specific name *biflagellatus*, a combination from Latin *bis* = twice and *flagellum* = a whip, refers to the two setiform processes on the segment of leg 5 in the female.

zavavy, Nosy Bé, Madagascar. Collected by A. G. Humes May 11, 1964. Holotype female, allotype, and 22 paratypes (19 females and 3 males) deposited in the United States National Museum, Washington; one paratypic female in the Museum of Comparative Zoology, Cambridge, Mass.; and the remaining paratypes in the author's collection.

Female.—The length of the body (excluding the setae on the caudal rami) is 1.63 mm (1.51–1.80 mm) and the greatest width (in the cephalosome, although in some specimens the segment of leg 2 may be expanded laterally so that its width is slightly greater) is 0.56 mm (0.51–0.61 mm), based on 5 individuals. The prosome is not much broadened, and somewhat longer than the urosome, the ratio being about 1.46 : 1 (Fig. 190). In dorsal aspect the epimera of the segments of legs 1–4 are conspicuously angulate. The segment bearing the fifth legs has a posterior transverse ridge, and bears a pair of prominent posterolateral recurved setiform processes about 100 μ long, with delicate hyaline lateral hairs (?). These processes are perhaps true setae, but an articulation could not be established with certainty. A very narrow intersegmental sclerite, more evident in a ventral view, occurs between the first two segments of the urosome. The genital segment (Fig. 191) is elongated, with two rounded lateral wings in its anterior fourth and with the sides of the posterior three-fourths subparallel and only very slightly swollen. An extremely indistinct transverse indication of subdivision occurs internally near the middle of the segment in some specimens. The genital segment measures 294 μ in dorsal length; its width at the anterior lateral expansions is 270 μ, and in the posterior third 167 μ.

The egg sacs are attached dorsolaterally on the two expansions of the genital segment, the actual attachment being covered by a dorsal flange (Fig. 192). Near the point of attachment there are two strongly sclerotized spine-like processes each about 6 μ in length. Each egg sac (Fig. 190) is elongated, about 519 × 170 μ, and contains numerous small eggs.

The three postgenital segments measure, respectively, 122 × 143, 84 × 130, and 78 × 108 μ. There is no apparent anal operculum. The anal segment bears on its dorsal and ventral surfaces fine hairs, as indicated in the figure. The caudal rami are inserted dorsally and the posterior ventral border of the segment below each ramus bears an outer row of minute spinules and an inner submarginal row of prominent spinules (the longest about 15 μ in length), as shown in Figure 193.

The dorsal surface of the prosome and the dorsal and ventral surfaces of the urosome bear minute hairs and refractile points.

The caudal ramus (Fig. 193) is moderately elongated, 100 μ in length, 41 μ wide just proximal to the lateral seta and 35 μ wide distal to that seta. Taking the width as 41 μ, the ramus is 2.44 times longer than wide. A minute hyaline hair arises on the outer basal margin. The lateral seta (52 μ long) and the outermost terminal seta (90 μ long) are both composed of a basal shaft and a distal flagelliform part. The dorsal seta is 200 μ long and bears a few lateral hairs. The innermost terminal seta is 227 μ in length and bears lateral spinules, those on the inner side being slightly better developed. The inner long terminal seta is 746 μ and the outer one 407 μ in length, both bearing lateral hairs (see Fig. 190). The four terminal setae are inserted somewhat dorsally and the resulting terminal ventral flange on the ramus bears a row of minute spinules. Along the inner margin of the ramus there is a row of very slender setules. Both the dorsal and ventral surfaces of the ramus bear scattered hyaline hairs.

The rostral region (Fig. 194) is well defined and bears a pair of setules and pairs of small hairs as indicated.

The first antenna (Fig. 195) is about 410 μ long, 7-segmented, the segments, beginning at the base, 15, 54, 49, 85, 58, 54, and 52 μ in length (measured along their non-setiferous margins). The armature is 4, 15, 6, 3, 4 + 1 aesthete, 2 + 1 aesthete, and

7 + 1 aesthete (the same formula as in *H. axiophilus*, *H. amplicaudatus*, *H. diremptus*, and *H. kombensis*). A few of the setae on the second segment show very short lateral hairs. On the distal posteroventral surface of this segment there are a few short rows of minute refractile points. Certain setae bear long lateral hairs as in *H. kombensis*.

The second antenna (Fig. 196) is 4-segmented, with the third segment produced on the inner distal corner where it bears four elements: proximally a slender posterior seta, more distally a long recurved seta (which resembles the four long terminal recurved setae on the last segment), and distally two unequal recurved spines, both bearing subterminal setules and the longer one a row of prominent spinules. The fourth segment is nearly quadrate, 33 × 30 μ, and bears seven setae much like those in *H. kombensis*.

The labrum (Fig. 197), in addition to ornamentation suggesting that in *H. kombensis*, shows a crescentic row of long hyaline setules, with the surface posterior to this row bearing conspicuous obtuse scales. The metastomal areas have a complex ornamentation, as shown in Figure 198.

The mandible (Fig. 199) has two stout elements and two well-developed setae with lateral hairs. The paragnath (Fig. 200) is a moderately elongated lobe bearing long hairs (shorter at the tip) and a row of small spinules as indicated. The first maxilla (Fig. 201) is in general similar to that of *H. kombensis*. The second maxilla (Fig. 202) also resembles in major features that of *H. kombensis*. The maxilliped (Fig. 203) is also much like that of *H. kombensis*, but the second segment is relatively longer and more slender, and the setae (including the two terminal claw-like setae) tend to be relatively longer. From near the base of the shorter claw-like seta there arises a setiform process without clear articulation. Between the bases of the maxillipeds there is a conspicuous ventral transverse sclerotization as shown in Figure 198.

The area between the maxillipeds and the first pair of legs is without conspicuous features.

The armature of legs 1–4 (Figs. 204, 205, 206, and 208) is as follows:

	protopod			exp			end		
P1	0:1	1:I	exp	I:0	I:1	I,I,6			
			end	0:1	0:1	I,5			
P2	0:1	1:0	exp	I:0	I:1	II,7			
			end	0:1	0:2	I,II,3			
P3	0:1	1:0	exp	I:0	I:1	II,I,6			
			end	0:1	0:2	I,II,3			
P4	0:1	1:0	exp	I:0	I:1	I,7			
			end	0:1	0:2	I,II,2			

This formula is somewhat different from that of *H. axiophilus*, the third exopod segment of leg 1 having two spines and the same segment in leg 3 having three spines. In leg 1 the inner spine on the basis is 105 μ in length, with short lateral spinules and with a blunt tip. The margin of the basis medial to this spine is rounded and smooth except for a tooth-like process near the base of the spine. In legs 2–4 this inner area of the basis bears a row of marginal hairs and a group of slender hyaline spinules on its anterior surface. The ventral margin of the intercoxal plate of leg 1 bears on each side rows of long hairs, but in legs 2–4 these hairs are replaced by spinules. The outer margin of the coxa of leg 4 lacks the long spinules seen on legs 1–3, but a row of slender spinules occurs on the outer posterior margin. In leg 3 the distalmost spine on the last segment of the exopod is distinctly spine-like rather than almost setiform as in *H. kombensis*. (An abnormal second segment of the exopod of leg 3, with two outer spines instead of one, is shown in Fig. 207.) On the last segment of the endopod of leg 4 the inner two elements are different from the outer three: the inner one being almost spine-like with lateral hairs basally and with a bilateral fringe of spinules in the distal three-fourths, the outer one being setiform with lateral hairs.

Leg 5 (Fig. 209) has a free segment which is somewhat constricted basally, broadened in the middle, and narrowed beyond the first outer spine. Its greatest length is 120 μ (91 μ along the outer edge to the base of the first spine and 94 μ along

the inner edge), and its greatest width is 56 μ. The ratio of greatest length to width is 2.14 : 1. There are rows of prominent spinules on both outer and inner margins. The three spines are 63, 59, and 71 μ in length, respectively, from outer to inner. The first few inner lateral spinules on the innermost spine are unusually long. The outermost spine seems to lack outer spinules. The seta is 93 μ long and bears a few lateral hairs. The basal area of leg 5 suggests a discrete segment; it is armed with a plumose seta about 100 μ in length and a group of outer spinules.

Leg 6 is apparently absent.

The color in living specimens, in transmitted light, is slightly opaque, with reddish orange globules in the prosome, the eye dark red, the ovary gray, the egg sacs dark reddish orange.

Male.—The length of the body (not including the setae on the caudal rami) is 1.34 mm (1.25–1.46 mm) and the greatest width is 0.45 mm (0.41–0.50 mm), based on 5 individuals. The prosome is less expanded than in the female (Fig. 210). The ratio of the length of the prosome to that of the urosome is about the same as that in the female. The segment of leg 5 lacks the two setiform processes seen in the female. The genital segment (Fig. 211) is wider than long, 148 × 178 μ, with gently rounded lateral margins.

The four postgenital segments measure, respectively, 108 × 103, 95 × 101, 62 × 98, and 54 × 89 μ.

As in the female, the prosome and urosome bear hairs and refractile points.

The caudal ramus is similar to that of the female, but is relatively shorter, the greatest length being 80 μ, the width just proximal to the lateral seta 35 μ, and the width distal to that seta 31 μ. Taking the width as 35 μ, the ramus is 2.29 times longer than wide.

The spermatophore (Fig. 212), as seen attached to the female, is pyriform, 68 μ long (including the slender neck of 6 μ) and 40 μ wide.

The rostral area is like that of the female. The first antenna resembles that of the female, but, as in previous species, has an additional seta on the third and fourth segments, so that the formula is 4, 15, 7, 4, 4 + 1 aesthete, 2 + 1 aesthete, and 7 + 1 aesthete.

The second antenna is similar to that of the female.

The labrum (Fig. 213) lacks the crescentic row of hyaline spinules, and the medial posteroventral surface has numerous scales and spinules, as shown in the figure. The metastomal areas (Fig. 214) are ornamented as indicated in the figure.

The mandible is like that in the female. The paragnath (Fig. 214) resembles that of the female, but seems to be somewhat more slender. The first maxilla is similar to that of the female. The second maxilla (Fig. 215) shows the stout inner element on the second segment here replaced by a strongly sclerotized, rather blunt, claw-like structure, sometimes pale yellowish in color, which lacks an articulation with the segment.

The maxilliped (Fig. 216) has a single long seta on the first segment. The second segment has its proximal inner angle expanded and rounded; the length of this segment along the outer margin is 137 μ, its greatest length from the distal end to the tip of the inner expansion is 173 μ, and its greatest width is 115 μ. There are three rows of fairly stout spines along the inner margin, in addition to the usual two setae. The third segment is very short and unarmed. The fourth segment forms part of the long recurved claw 189 μ in length (measured along its axis and not along its curvature), bearing near its base on the posterior surface a small seta 18 μ long, and on its inner curvature a spinous process 25 μ long and a minute setule 5 μ long. The ventral surface of the cephalosome between the bases of the maxillipeds (Fig. 217) shows only an incomplete transverse line, instead of the readily visible sclerotization seen in the female.

Leg 1 lacks the inner spine on the basis (Fig. 218). Otherwise legs 1–4 show the same spine and setal formula as in the fe-

male. The last endopod segments of legs 2 and 3 (Figs. 219 and 220) show the three terminal processes reduced and blunt, in contrast to their acute spiniform condition in the female.

Leg 5 (Fig. 221) has a free segment which is relatively longer and more slender than in the female. Its greatest length is 116 μ (81 μ along the outer edge to the base of the first spine and 93 μ along the inner edge) and its greatest width is 44 μ. The armature resembles in major respects that of the female, although the outermost spine has spinules along both sides. The basal area of leg 5 does not seem to show a clear separation from the body.

Leg 6 (Fig. 222) consists of a ventral flap on the posterior part of the genital segment, bearing a strong spine 44 μ in length. In a dorsal view of the animal this spine projects posterolaterally beyond the edge of the segment.

The color in life resembles that of the female.

Remarks on its biology.—*H. biflagellatus* was collected on only one occasion, and then from burrows which also contained *H. diremptus* and *H. carinifer.*

Relationship to other species.—This species seems to be unique among the previously described species of the genus in having two posterolateral setiform processes on the segment of leg 5. Otherwise, it resembles *H. thysanotus* Wilson, 1935, in certain respects. However, in the female of *H. thysanotus* the inner spine on the basis of leg 1 is recurved and rather blunt instead of straight, and in the male the form of the maxilliped is rather different from that of the Madagascar species. *H. biflagellatus* is unlike *H. leggii* (Thompson and Scott, 1903), of which only the male is known; in this species the caudal rami are nearly quadrate and the basal segment of the male maxilliped has two setae. *H. bacescui* (Şerban, 1956) has, in the female, less prominent expansions on the genital segment and the inner spine on the basis of leg 1 has strong denticulations. *H. purpureus* Boeck, 1873, has, in the female, a broader distal

segment in leg 5 and shorter caudal rami, and the inner distal corner of the third segment of the second antenna is not prolonged. *H. thompsoni* (Canu, 1888) has a broad distal segment of leg 5 in the female.

The following species also has a pair of setiform processes on the segment of leg 5, but may be readily distinguished from *H. biflagellatus* as pointed out below.

Hemicyclops acanthosquillae[1] n. sp.

Pl. XXXII, figs. 223–227; Pls. XXXIII–XXXVI

Type material.—8 females and 5 males washed from the bodies of two stomatopods, *Acanthosquilla* sp., dug from intertidal sand at Antsakoabe, on the northwestern shore of Nosy Bé, Madagascar. Collected by A. G. Humes July 12, 1964. Holotype female, allotype, and 8 paratypes (5 females and 3 males) deposited in the United States National Museum, Washington; one paratypic female in the Museum of Comparative Zoology, Cambridge, Mass.; and the remaining paratypes in the author's collection.

Female.—The length of the body (not including the setae on the caudal rami) is 2.24 mm (2.00–2.44 mm) and the greatest width (taken at the level of the segment bearing leg 2) is 0.71 mm (0.68–0.80 mm), based on 5 individuals. The prosome is moderately broadened and of about the same length as the urosome (Fig. 223). In dorsal aspect the epimera of the segments of legs 1–4 are angulate posterolaterally. The segment bearing the fifth legs is rounded laterally and bears a pair of posterolateral smooth setiform processes about 72 μ in length (Figs. 224 and 225). (These resemble somewhat the two setiform processes described in the preceding species.) Medial to the two processes there is a pair of minute hyaline setules (hairs?) about 8 μ long. An intersegmental sclerite may be seen ventrally between the first two urosomal segments. The genital segment (Fig. 224) is

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[1] The specific name *acanthosquillae* is taken from the generic name of the crustacean upon whose body the copepod was found.

greatly elongated. In dorsal view it shows two pronounced lateral swellings in its anterior fifth, the remaining portion of the segment having the sides nearly parallel. Dorsally, just anterior to the midregion, there are four longitudinally oblique sclerotizations. The segment measures 486μ in length; its width at the level of the two swellings is 289μ, and in the posterior part 224μ.

The egg sacs are attached slightly dorsally on the lateral swellings of the genital segment, between dorsal and ventral flanges. Each egg sac is elongated (Fig. 223), about $730 \times 235 \mu$, and contains many small eggs, each about 53μ in diameter.

The three postgenital segments measure, respectively, 243×205, 159×159, and $100 \times 135 \mu$. There is no evident anal operculum. The anal segment is provided ventrally on each side along its posterior margin with an outer row of minute spinules and an inner row of spines (see Fig. 226). The dorsal surface of the urosome bears minute refractile points and hairs as shown in Figure 224.

The caudal ramus (Fig. 226) measures $116 \times 54 \mu$ (2.15 times longer than wide). All six setae are inserted somewhat dorsally. There is a minute hyaline hair on the basal outer margin. The lateral seta (58μ long) and the outermost terminal seta (103μ long) are both composed of a distinct basal shaft and a distal flagelliform part. The sparsely haired dorsal seta is 95μ in length. The innermost terminal seta is 282μ in length and bears lateral spinules. The inner long terminal seta is 1017μ and the outer one 542μ in length, both bearing lateral hairs (see Fig. 223). The posterior end of the ramus is prolonged ventrally to form a flange bearing a row of minute spinules and, near the base of the innermost terminal seta, a row of larger spinules. The distal half of the inner margin of the ramus bears a row of very slender spinules.

The rostral area (Fig. 227) is well defined and bears a pair of setules.

The first antenna (Fig. 228) is about 441μ long, 7-segmented, the segments, be-

ginning at the base, being 15, 68, 49, 94, 59, 58, and 54μ in length (measured along their non-setiferous margins). The armature is similar to that of *H. biflagellatus*.

The second antenna (Figs. 229 and 230) is 4-segmented, with the third segment much produced on the inner distal corner, where it bears four elements: proximally a slender seta, more distally a stout recurved seta, and terminally two recurved unequal spines, both provided with subterminal setules and the longer one having a row of spinules. The fourth segment is quadrate, $23 \times 23 \mu$, and bears the usual seven setae. The convex inner area of the second segment bears on its posterior surface numerous scale-like protuberances, and the concave inner area of the third segment bears also on its posterior surface short spine-like knobs (see Fig. 230).

The labrum (Fig. 231) has a group of broad irregular ventromedial lobes, in addition to the other ornamentation shown in the figure. The metastomal areas have a complex ornamentation, as indicated in Figure 232.

The mandible (Fig. 233) has the usual two stout elements and two well-developed setae with lateral spinules. The paragnath (Fig. 234) is a moderately elongated lobe with hairs and short spinules as indicated in the figure. The first maxilla (Fig. 235) resembles in major respects that of *H. biflagellatus*. The second maxilla (Fig. 236) is similar to that of the preceding species. The maxilliped (Fig. 237) also resembles in general structure that of the preceding species, but there is a greater number of small hyaline setae near the bases of the two terminal claw-like setae. There is a conspicuous ventral transverse sclerotization between the bases of the maxillipeds (see Fig. 232) as in *H. biflagellatus*.

The area between the maxillipeds and the first pair of legs lacks outstanding features.

The armature of legs 1–4 (Figs. 238, 240, 242, and 243) is similar to that of *H. axiophilus*. In leg 1 the inner spine on the basis is 52μ in length, with short truncated lateral spinules, giving the edges the ap-

pearance of a saw blade (Fig. 239). The margin of the basis medial to this spine is smooth, except for a rather blunt tooth-like process near the base of the spine. In legs 2–4 this inner area of the basis bears a row of marginal hairs and a group of slender hyaline setules on its anterior surface. As in the preceding species, the ventral margin of the intercoxal plate of leg 1 bears hairs, while in legs 2–4 it bears spinules; and the coxa of leg 4 lacks the long slender spinules seen in legs 1–3, instead having a row of spinules on the outer posterior margin. In leg 1 the outer margin of the second segment of the endopod bears only a row of hairs, but in legs 2–4 this margin bears basally a group of small knobs (Fig. 241) followed by the usual hairs. On the last endopod segment of leg 4 the inner two elements are setae, the lateral hairs on the innermost being equal but those on the adjacent seta being longer near the base and shorter on the distal three-fourths of the seta; the fringed inner terminal spine is more than twice as long as either the outer terminal spine or the outer lateral spine.

Leg 5 (Fig. 244) has a free segment which is narrow basally but broadened distally, its greatest dimensions being 142 × 95 μ, with a ratio of length to width of 1.5 : 1. There are rows of long spinules on both outer and inner edges of the segment. The three spines measure 67, 73, and 86 μ in length, respectively, from outer to inner; the seta is 88 μ long. The basal area of the leg suggests a discrete segment and is armed as in the preceding species.

Leg 6 is apparently absent.

The color in living specimens in transmitted light is slightly amber, with the eye red and the egg sacs gray. The spermatophores attached to the female are golden brown.

Male.—The length of the body (not including the setae on the caudal rami) is 1.85 mm (1.79–1.91 mm), and the greatest width is 0.63 mm (0.60–0.66 mm), based on 5 individuals. The prosome is only slightly less expanded than in the female, and is somewhat longer than the urosome (Fig.

245), the ratio being 1.2 : 1. The segment of leg 5 lacks the two setiform processes seen in the female, but instead has dorsally on each side, medial to the seta associated with the leg, a somewhat triangular projection (Figs. 246 and 247). The genital segment (Fig. 246) is about as long as wide, 260 × 271 μ, with gently rounded lateral margins.

The four postgenital segments measure, respectively, 186 × 157, 157 × 130, 108 × 116, and 76 × 116 μ.

The dorsal surface of the urosome bears hairs and refractile points, as indicated in the figure.

The caudal ramus resembles that of the female, but is relatively shorter, the greatest dimensions being 92 × 49 μ. The ratio of length to width is 1.88 : 1.

The spermatophore (Fig. 248), as seen attached ventrally on the genital segment of the female, is somewhat irregularly ovoid. Its greatest dimensions are 124 × 99 μ plus a neck of 13 μ.

The rostral region (Fig. 249) is only slightly less defined than that of the female.

The first antenna resembles that of the female, but, as in previous species, has an additional seta on the third and fourth segments, thus giving the formula of 4, 15, 7, 4, 4 + 1 aesthete, 2 + 1 aesthete, and 7 + 1 aesthete.

The second antenna is like that of the female.

The labrum (Fig. 250) has a more complex ornamentation than in the female. The metastomal areas (Fig. 251) are ornamented as shown in the figure.

The mandible resembles that of the female. The paragnath appears to be similar to that of the female, but the notch on the outer edge is less apparent. The first maxilla is like that of the female. The second maxilla (Fig. 252), as in previous species, has the stout inner element on the second segment transformed to form a strongly sclerotized, rather blunt, claw-like structure, having a conspicuous yellowish amber color and lacking an articulation with the segment.

The maxilliped (Fig. 253) has a single long seta on the first segment. The second segment has its proximal inner angle rather acutely expanded. The length of this segment along its outer margin is 197 μ, its greatest length from the distal end to the tip of the inner expansion is 240 μ, and its greatest width is 159 μ. There are three rows of moderately stout but somewhat obtuse spines along the inner surface, plus the usual two setae. The third segment is very short and unarmed. The fourth segment forms part of the long, slightly recurved claw, 235 μ in length (measured along its axis and not along its curvature). The claw bears near the base on its posterior surface a slender seta 35 μ in length, and on its inner curvature a spinous process 28 μ long and a minute setule 10 μ long. The ventral surface of the cephalosome between the bases of the maxillipeds shows only an incomplete transverse line (Fig. 251), as in *H. biflagellatus*.

Leg 1 lacks the inner spine on the basis (Fig. 254) and the spinules in this region are longer and more slender than in the female. Otherwise legs 1–4 have the same spine and setal formula as in the female. The sclerotization of the rami appears to be stronger than in the opposite sex.

Leg 5 (Fig. 255) has an elongated free segment which is relatively much more slender than in the female. Its greatest dimensions are 132 × 57 μ, the ratio of length to width being about 2.3 : 1. The ornamentation resembles that of the female, but the lateral spinules on the three terminal spines are shorter. The basal area of leg 5 does not show a separation from the body. Leg 6 (Fig. 256) consists of a ventral sclerotized flap on the posterior region of the genital segment, bearing an outwardly directed spine 38 μ in length with minute lateral spinules on each side. This spine in dorsal view of the body projects posterolaterally beyond the edge of the genital segment (see Figs. 245 and 246).

The color in life resembles that of the female.

Remarks on its biology.—The two stomatopods from which these copepods were taken appeared in the water seeping into a hole 30 cm deep which had been dug in clean sand. They were quickly placed in a plastic bag with a small amount of sea water. Later a few drops of ethyl alcohol were added, the whole gently agitated, and the copepods recovered from the sediment. There seems to be justification for assuming that these *Hemicyclops* were living on the bodies of the *Acanthosquilla*. This is the first record of a member of the genus *Hemicyclops* occurring on a stomatopod.

Relationship to other species.—*H. acanthosquillae* belongs to the group of *Hemicyclops* species having four setae on the first segment of the first antenna. It possesses several very characteristic features by which it may be distinguished from other members of this group: on the segment of leg 5 in the female a pair of dorsolateral setiform processes and in the male a pair of triangular projections; the form, armature, and ornamentation of the second antenna, especially the greatly produced inner distal corner of the third segment and the very small quadrate fourth segment; the ornamentation of the outer edge of the second segment of the endopods of legs 2–4; and the acute inner proximal expansion of the second segment of the male maxilliped.

H. acanthosquillae bears certain resemblances to *H. biflagellatus*. For example, in the female, the elongated genital segment has anterior lateral expansions and there is a pair of setiform processes on the segment of leg 5. It may be distinguished from *H. biflagellatus*, however, by several readily observable characters, such as the form of the second antenna, the fifth leg, and the male maxilliped.

REMARKS ON THE SPECIES OF *HEMICYCLOPS* FROM MADAGASCAR

Gooding (1960) divided the American species of *Hemicyclops* into two groups on the basis of morphological characters. Later (1963, unpublished thesis), he developed further this concept of groups of species within the genus. Selecting a few typical

characters, the eight known species from Madagascar (comprising the seven described above and *H. visendus*) may be placed in two groups (corresponding to two of Gooding's):

1) those species with the urosome of the adult female having five segments, with four setae on the first segment of the first antenna, with a short terminal segment on the second antenna, and with a sexually dimorphic second maxilla, including:

H. axiophilus n. sp.
H. amplicaudatus n. sp.
H. diremptus n. sp.
H. kombensis n. sp.
H. biflagellatus n. sp.
H. acanthosquillae n. sp.
H. visendus Humes, Cressey,
and Gooding, 1958;

2) that species with the urosome of the adult female having six segments, with five setae on the first segment of the first antenna, with an elongate terminal segment on the second antenna, and without sexual dimorphism in the second maxilla:

H. carinifer n. sp.

THE GENUS *HEMICYCLOPS* IN THE INDIAN OCEAN

Five species of *Hemicyclops* have been reported from the Indian Ocean area: *H. indicus* Sewell, 1949, from Nankouri Harbour, Nicobar Islands, in weed-washings; *H. leggii* (Thompson and Scott, 1903) in washings from dredgings, sponges, in the Gulf of Manaar, Ceylon; *H. intermedius* Ummerkutty, 1962, from weed-washings in the Gulf of Manaar, southeastern coast of India; *H. tamilensis* (Thompson and Scott, 1903) in Muttuvaratu pearl oyster washings, Ceylon; and *H. visendus* Humes, Cressey, and Gooding, 1958, from *Upogebia* sp. at Nosy Bé, Madagascar.

In addition, Pillai (1963) has reported *Hemicyclops* sp. from brackish water at Ashtamudi Lake, Quilon, Kerala State, India. The only specimen, a male, is 2.3 mm in length and belongs to the group of species having four setae on the first segment

of the first antenna. Its size alone distinguishes it from all six of the species in this group from Madagascar described above. The caudal ramus is nearly three times longer than wide (in *H. amplicaudatus* it is 3.6 times, in *H. axiophilus*, *H. diremptus*, *H. kombensis*, *H. biflagellatus*, and *H. acanthosquillae* it is 2.4 times or less). The male of *H. kombensis* appears to be closest to the Indian specimen, having a length of 2.09 mm and the caudal ramus being 2.4 times longer than wide. In the Indian form, however, the free segment of leg 5 is broader, the genital segment is not constricted anteriorly, and hairs occur along the entire inner border of the caudal ramus.

The question arises whether Pillai's specimen may be one of the five Indian Ocean species mentioned above. This male shows the fourth segment of the first antenna distinctly longer than the second (Pillai's fig. 49), while in *H. indicus* the reverse is true. The free segment of leg 5 is broadened and the second segment of the male maxilliped has its inner side rather angularly expanded proximally, while in *H. visendus* the free segment is elongate and the second segment of the maxilliped has its inner side broadly expanded. The caudal rami are nearly three times longer than wide and the first segment of the male maxilliped has one seta, while in *H. leggii* the caudal rami are nearly quadrate and the first segment of the maxilliped has two setae. The male of *H. tamilensis* is unknown, but the female of this Ceylonese species has nearly quadrate caudal rami, and it is perhaps safe to assume for the present that *H. tamilensis* and Pillai's single male are distinct.

Only the female of *H. intermedius* is known. It belongs to the group of *Hemicyclops* species having four setae on the first segment of the first antenna. It appears to be distinct from all six new species in this group described above. In these the caudal ramus is two or more times longer than wide, while in *H. intermedius* it is quadrate; the contour of the genital segment in dorsal view is different from that in *H. intermedius*; the inner distal corner of the third segment

of the second antenna is produced, while in *H. intermedius* this region is rounded; and the armature of the four legs is somewhat different than in *H. intermedius*, where, for example, the formula for the third exopod segment of the first leg is III,I,4.

It is difficult to compare *H. intermedius* and Pillai's *Hemicyclops* sp., since the corresponding sexes are not known. These two copepods seem to be distinct, however, since in the male *Hemicyclops* sp. the caudal rami are nearly three times longer than wide, the inner distal corner of the third segment of the second antenna is produced, and the armature of the third exopod segment of the first leg is I,7.

Twelve described species and one unnamed form of *Hemicyclops* are now known from the Indian Ocean area: *H. indicus* from the Nicobar Islands, *H. leggii* and *H. tamilensis* from Ceylon, *H. intermedius* and *H.* sp. from India, and *H. axiophilus, H. amplicaudatus, H. carinifer, H. diremptus, H. kombensis, H. biflagellatus, H. acanthosquillae,* and *H. visendus* from Madagascar.

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SCALE A. 1.0 MM

SCALE B. 0.3 MM

SCALE C. 0.5 MM

SCALE D. 0.1 MM

SCALE E. 0.1 MM
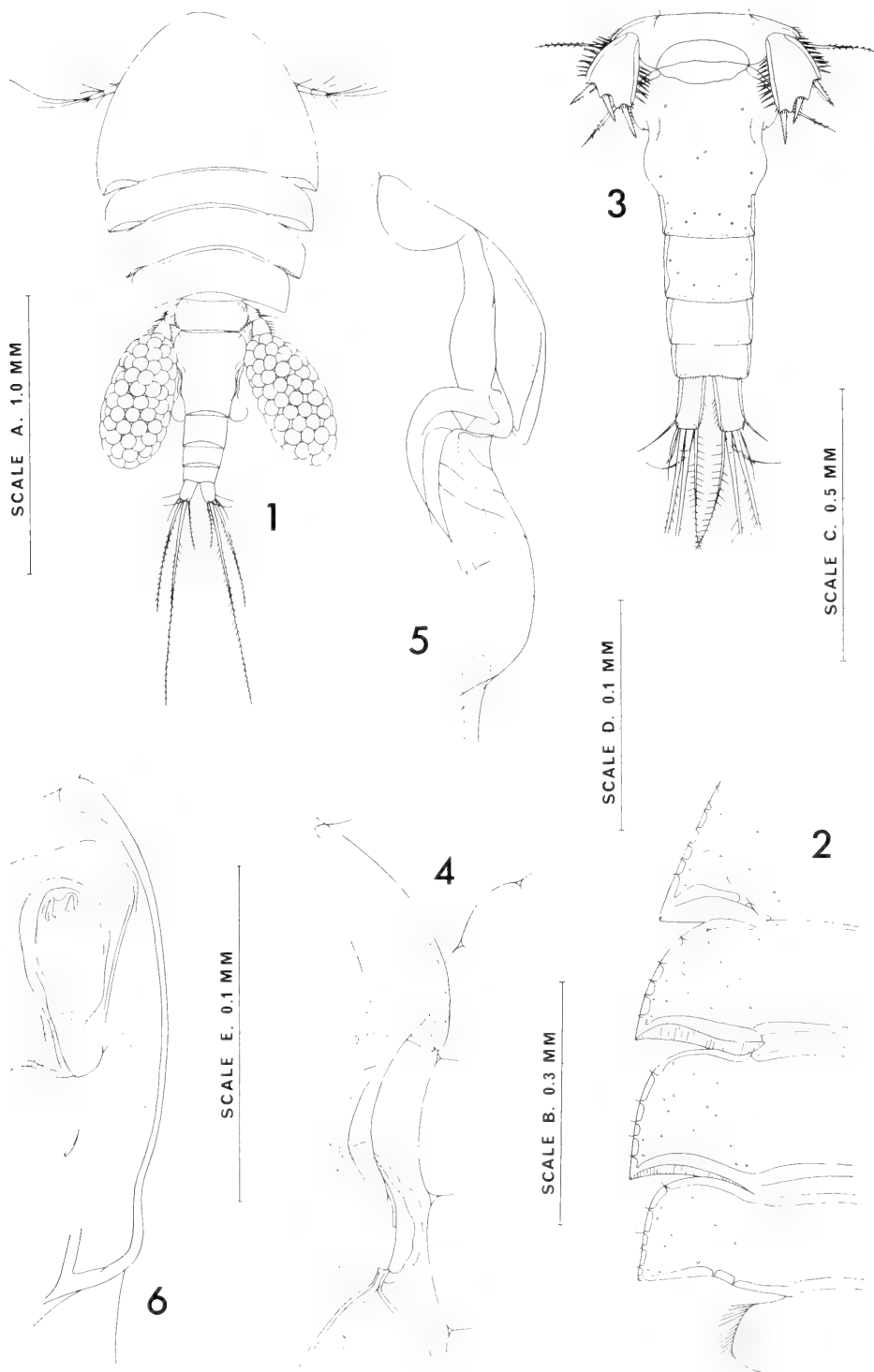
EXPLANATION OF FIGURES

All figures were drawn with the aid of a camera lucida. The letter after each figure refers to the scale at which it was drawn.

Plate I

Hemicyclops axiophilus n. sp., female

Fig. 1.   Body, dorsal (A).
Fig. 2.   Edges of somites of legs 1–5, dorsal (B).
Fig. 3.   Urosome, ventral (C).
Fig. 4.   Part of edge of genital segment showing areas of attachment of egg sac and spermatophore, ventral (D).
Fig. 5.   Part of edge of genital segment, dorsal (D).
Fig. 6.   Same, lateral (E).
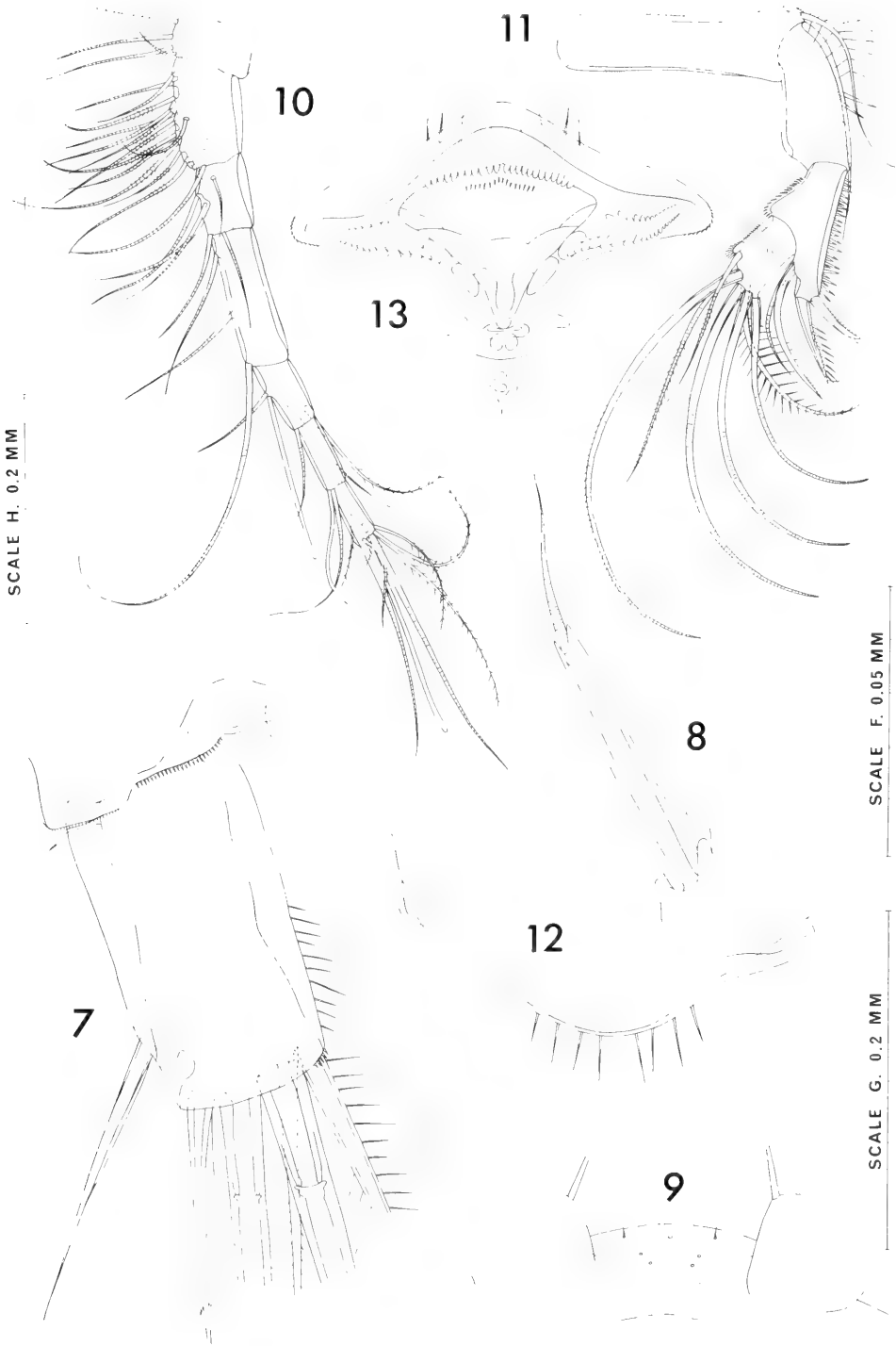
Plate II
Hemicyclops axiophilus n. sp., female (continued)

Fig. 7.   Caudal ramus, ventral (E).
Fig. 8.   Outermost terminal seta on caudal ramus, dorsal (F).
Fig. 9.   Rostral area, ventral (G).
Fig. 10.   First antenna, anterodorsal (H).
Fig. 11.   Second antenna, anterior or ventral (G).
Fig. 12.   Edge of labrum, anterior and dorsal (E).
Fig. 13.   Posterior surface of labrum, pushed forward (E).
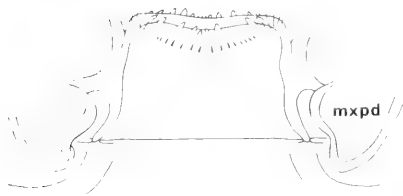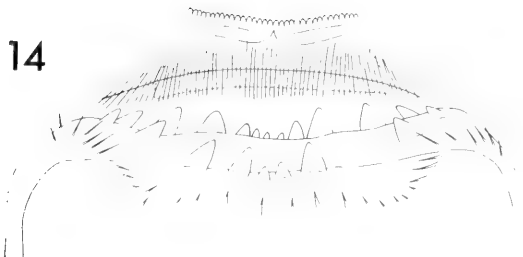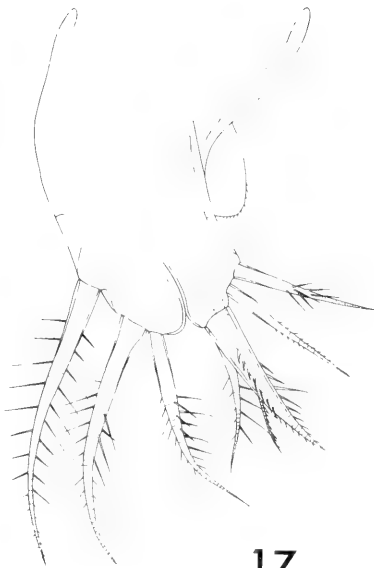
Plate III
Hemicyclops axiophilus n. sp., female (continued)
Fig. 14. Metastomal areas, ventral (E).
Fig. 15. Mandible, anterior and dorsal (E).
Fig. 16. Paragnath, anterior (E).
Fig. 17. First maxilla, posterior (E).
Fig. 18. Second maxilla, posterior (G).
Fig. 19. Maxilliped, anterior or dorsal (G).
Fig. 20. Region between maxillipeds and leg 1, ventral (H).

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22

24

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Plate IV
Hemicyclops axiophilus n. sp., female (continued)

Fig. 21. Leg 1, anterior (H).
Fig. 22. Leg 2, posterior (H).
Fig. 23. Leg 3, posterior (H).
Fig. 24. Leg 4, posterior (H).

32

a₁

a₂

md

p

mx₁

mx₂

mxpd

38

37

36

34

33

35

Plate VI

Hemicyclops axiophilus n. sp., male (continued)

Fig. 32. Part of cephalosome, ventral (H).
Fig. 33. Second maxilla, posterior (G).
Fig. 34. Distal segment of second maxilla, posterior (E).
Fig. 35. Maxilliped, anterior (dorsal of large segment and claw) (G).
Fig. 36. Maxilliped, posterior (ventral of large segment and claw) (G).
Fig. 37. Maxilliped, inner surface (G).
Fig. 38. Detail of part of leg 1, posterior (H).

Abbreviations

a_1, first antenna mx_1, first maxilla
a_2, second antenna mx_2, second maxilla
md, mandible   mxpd, maxilliped
p, paragnath p_1, leg 1
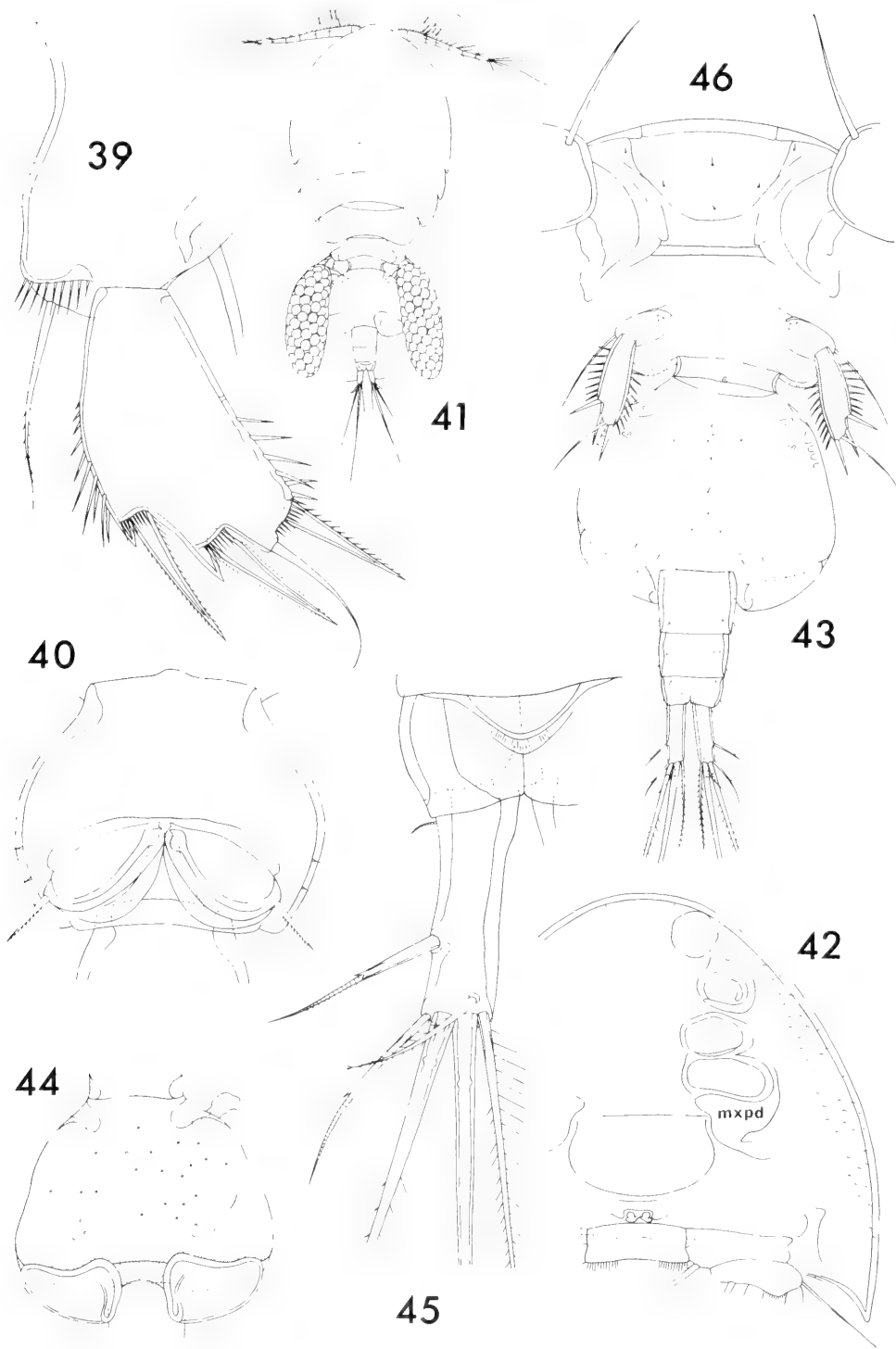
Plate VII
Hemicyclops axiophilus n. sp., male (continued)
Fig. 39. Leg 5, ventral (D).
Fig. 40. Genital segment showing leg 6, ventral (H).
Hemicyclops amplicaudatus n. sp., female
Fig. 41. Body, dorsal (A).
Fig. 42. Part of cephalosome, ventral (B).
Fig. 43. Urosome, ventral (B).
Fig. 44. Genital segment, dorsal (B).
Fig. 45. Caudal ramus and part of anal segment, dorsal (E).
Fig. 46. Rostral area, ventral (D).

Plate VIII
Hemicyclops amplicaudatus n. sp., female (continued)
Fig. 47.   First antenna, ventral (G).
Fig. 48.   Second antenna, posterior (G).
Fig. 49.   Last two segments of second antenna, posterior (E).
Fig. 50.   Oral area, ventral (E).
Fig. 51.   Mandible, ventral (E).
Fig. 52.   Mandible, dorsal (E).
Fig. 53.   Paragnath, ventral and posterior (F).
Fig. 54.   First maxilla, posterior (G).
Fig. 55.   Second maxilla, posterior (G).
Fig. 56.   Maxilliped, posterior and slightly outer (G).

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Plate IX
Hemicyclops amplicaudatus n. sp., female (continued)

Fig. 57. Leg 1, anterior (G).
Fig. 58. Leg 2, anterior (G).
Fig. 59. Leg 3, posterior (G).
Fig. 60. Leg 4, posterior (G).

Plate X
Hemicyclops amplicaudatus n. sp., female (continued)
Fig. 61. Leg 5, dorsal (D).

Hemicyclops amplicaudatus n. sp., male
Fig. 62. Body, dorsal (A).
Fig. 63. Urosome, dorsal (H).
Fig. 64. Segments 3 and 4 of first antenna, ventral (D).
Fig. 65. Second maxilla, anterior (D).
Fig. 66. Second maxilla, posterior (D).
Fig. 67. Maxilliped, anterior (D).
Fig. 68. Area between maxillipeds and leg 1, ventral (H).
Fig. 69. Portion of leg 1, anterior (G).
Fig. 70. Leg 5, ventral (D).
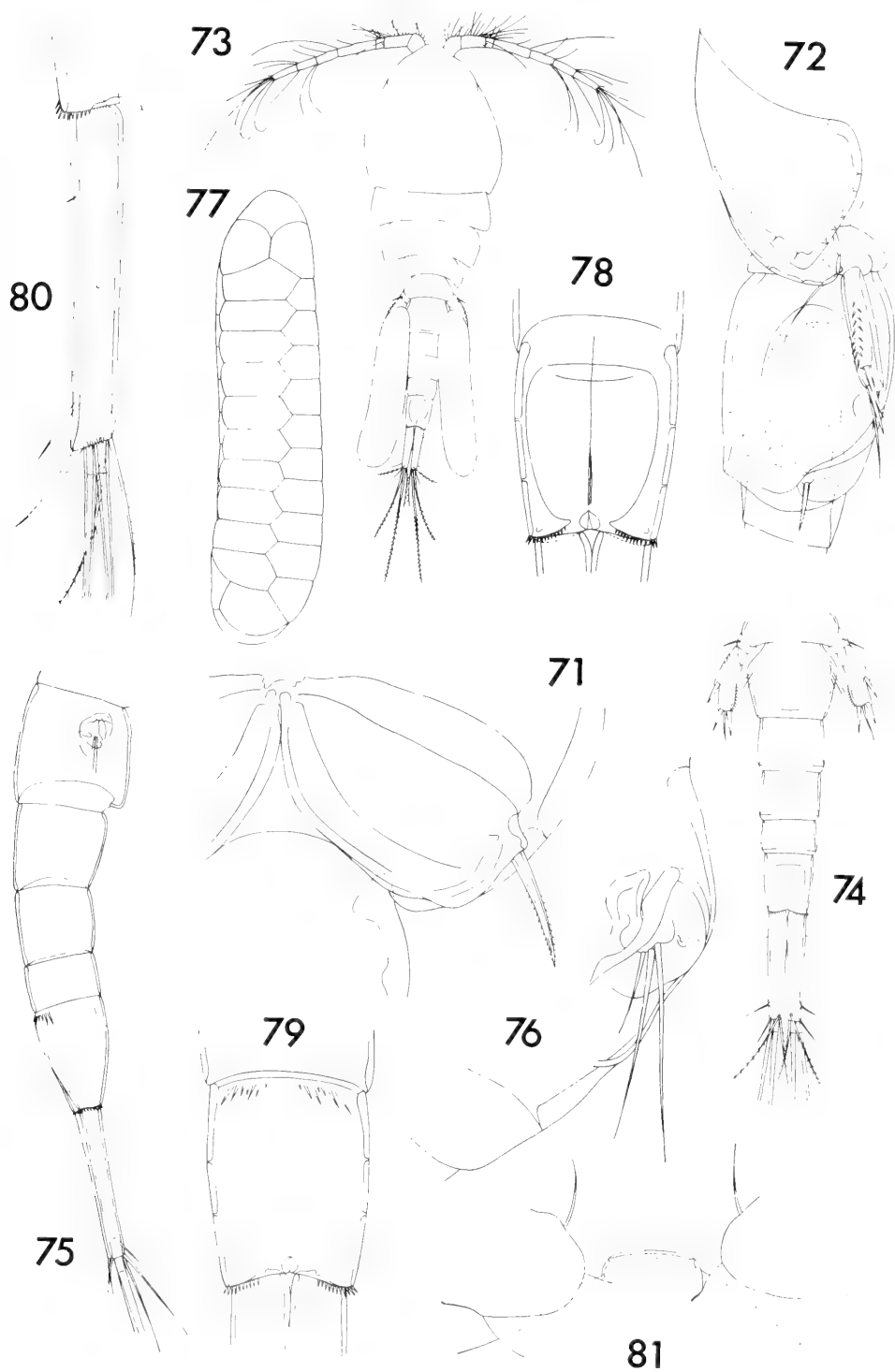
Plate XI
Hemicyclops amplicaudatus n. sp., male (continued)

Fig. 71. Leg 6, ventral (D).
Fig. 72. Segment of leg 5, genital segment, and adjacent areas, lateral (H).

Hemicyclops carinifer n. sp., female

Fig. 73. Body, dorsal (A).
Fig. 74. Urosome, dorsal (C).
Fig. 75. Urosome, lateral (B).
Fig. 76. Area of attachment of egg sac, dorsal and slightly lateral (E).
Fig. 77. Egg sac, dorsal (B).
Fig. 78. Anal segment, dorsal (G).
Fig. 79. Anal segment, ventral (G).
Fig. 80. Caudal ramus, ventral (G).
Fig. 81. Rostral area, ventral (D).

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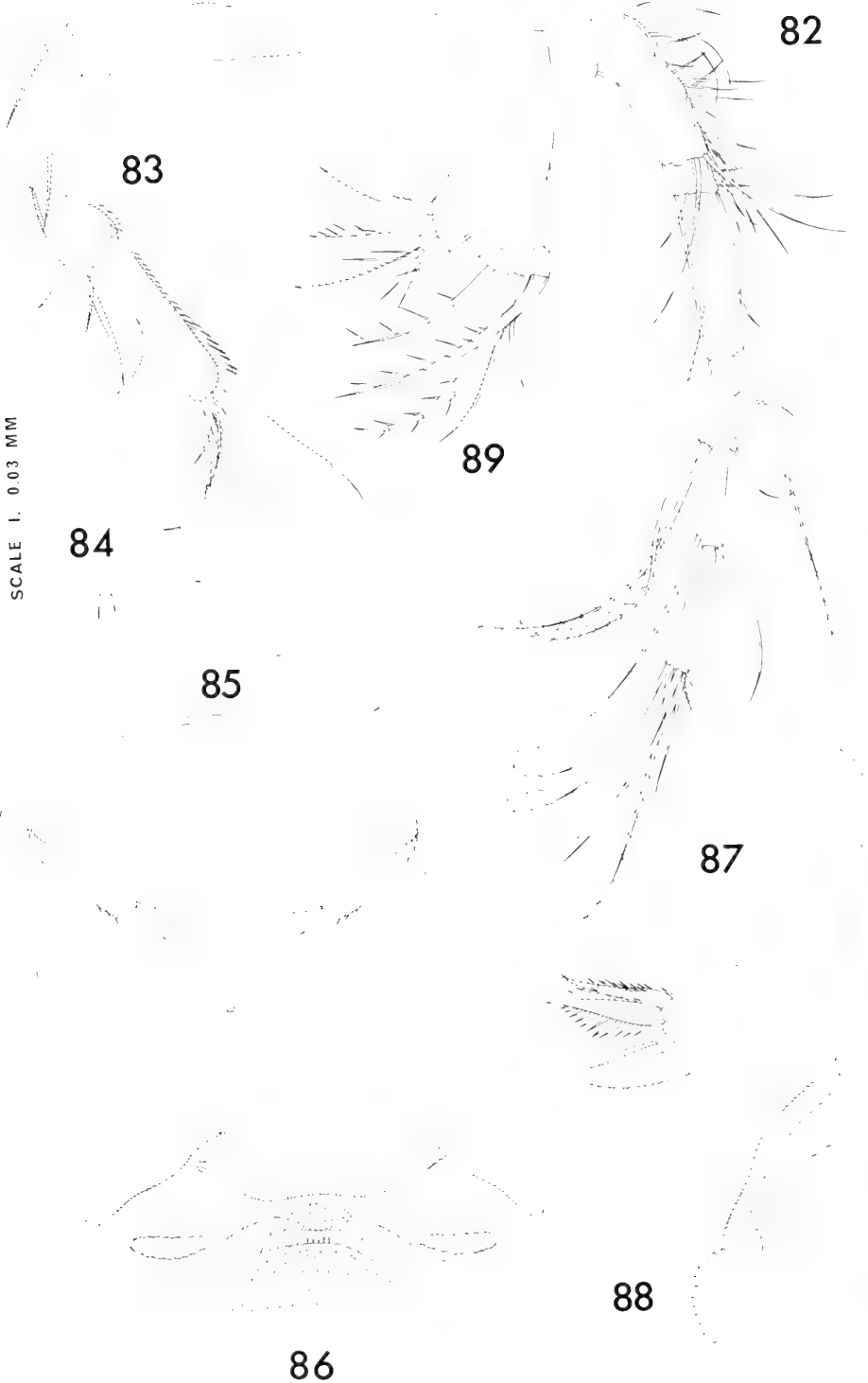
Plate XII
Hemicyclops carinifer n. sp., female (continued)

Fig. 82.   First antenna, dorsal (H).
Fig. 83.   Second antenna, posterior mesial (G).
Fig. 84.   Seta on third segment of second antenna (I).
Fig. 85.   Labrum, anterior and ventral (E).
Fig. 86.   Metastomal areas and paragnaths, ventral (E).
Fig. 87.   Mandible, posterior (E).
Fig. 88.   Paragnath, ventral and posterior (F).
Fig. 89.   First maxilla, posterior (E).
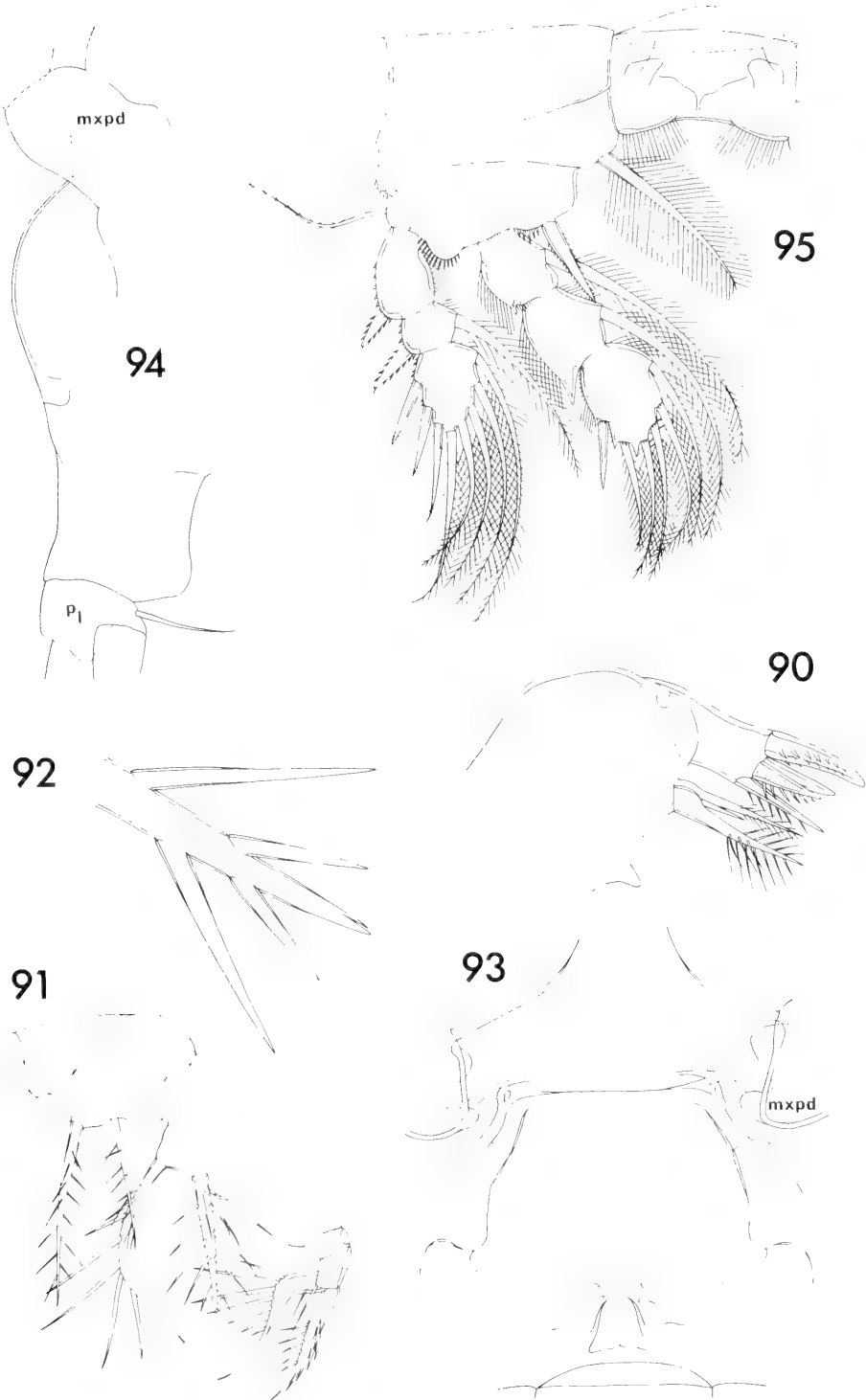
Plate XIII
Hemicyclops carinifer n. sp., female (continued)

Fig. 90.   Second maxilla, posterior and dorsal (D).
Fig. 91.   Maxilliped, dorsal (G).
Fig. 92.   Terminal part of distal seta on second segment of maxilliped (I).
Fig. 93.   Area between maxillipeds and leg 1, ventral (G).
Fig. 94.   Area between maxillipeds and leg 1, lateral (G).
Fig. 95.   Leg 1, anterior (G).
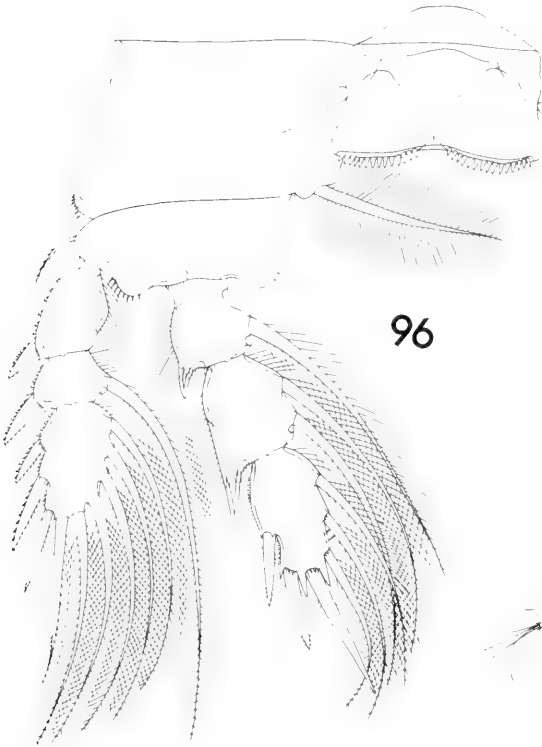
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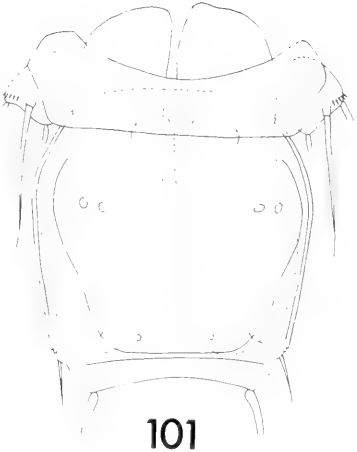
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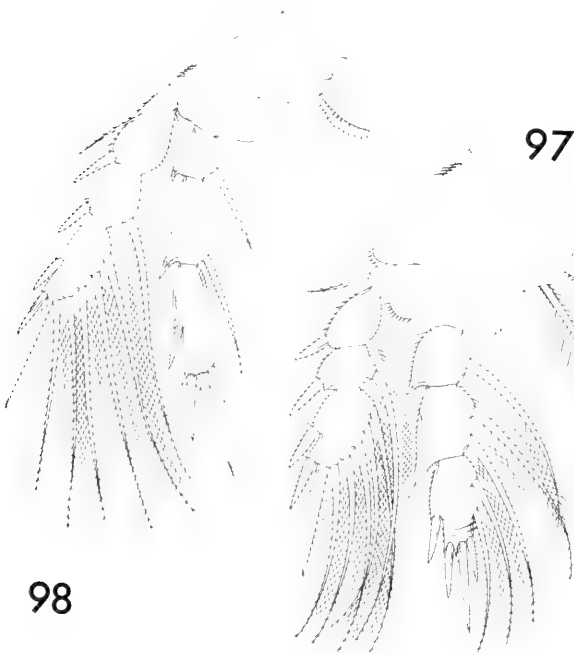
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Plate XIV
Hemicyclops carinifer n. sp., female (continued)

Fig. 96.   Leg 2, anterior (G).
Fig. 97.   Leg 3, posterior (H).
Fig. 98.   Leg 4, posterior (H).
Fig. 99.   Leg 5, ventral and lateral (D).

Hemicyclops carinifer n. sp., male

Fig. 100.   Body, dorsal (A).
Fig. 101.   Segment of leg 5 and genital segment, dorsal (G).

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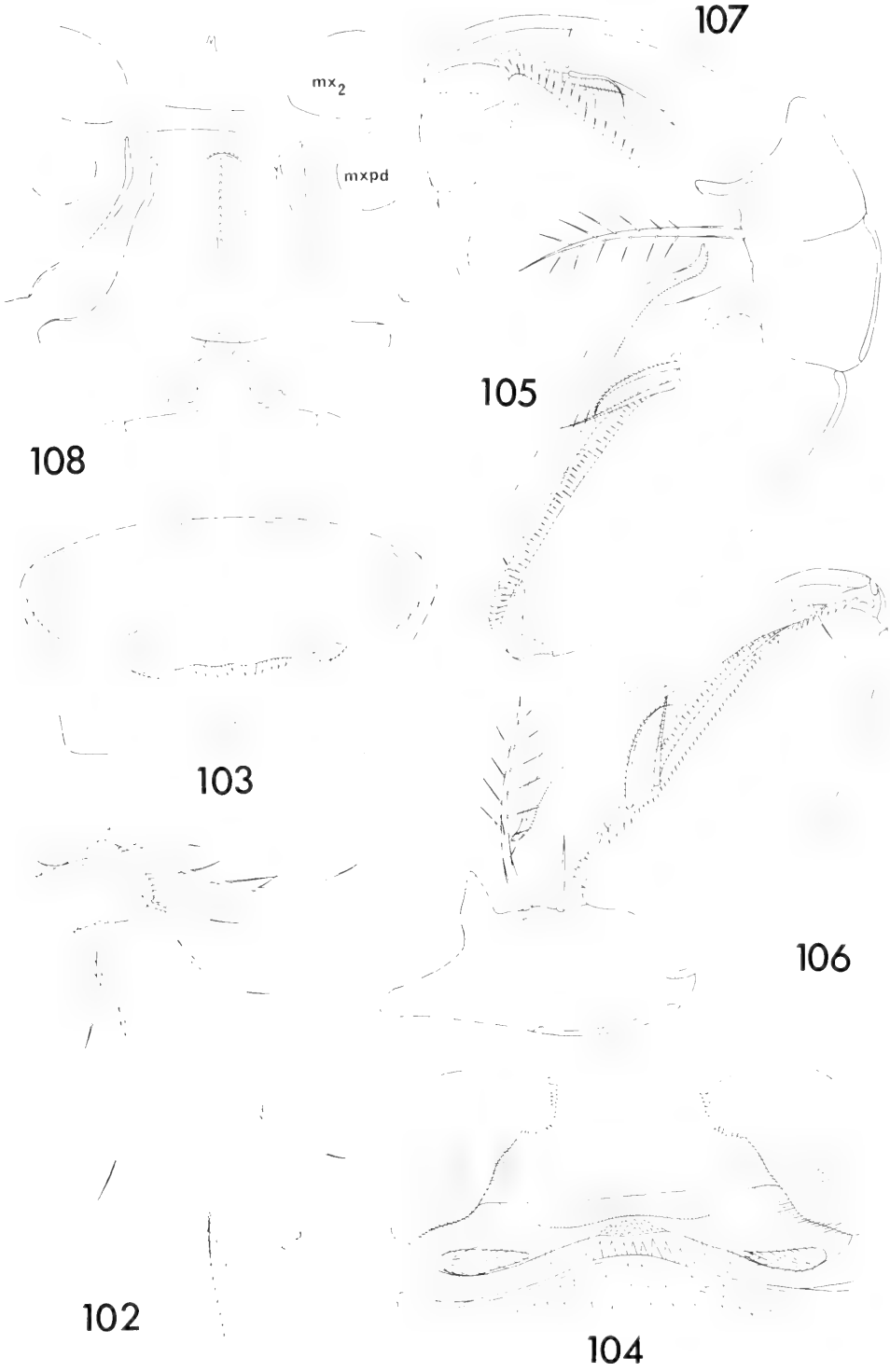
Plate XV
Hemicyclops carinifer n. sp., male (continued)

Fig. 102. Third and fourth segments of first antenna, dorsal (D).
Fig. 103. Labrum, ventral and anterior (E).
Fig. 104. Metastomal areas and paragnaths, ventral (E).
Fig. 105. Maxilliped, anterior (G).
Fig. 106. Maxilliped, posterior (G).
Fig. 107. Detail of third and fourth segments of maxilliped, anterior (E).
Fig. 108. Area between maxillipeds and leg 1, ventral (G).

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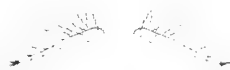
Plate XVI
Hemicyclops carinifer n. sp., male (continued)

Fig. 109. Area between maxillipeds and leg 1, lateral (G).
Fig. 110. Leg 1, anterior (G).
Fig. 111. Inner spine on basis of leg 1, posterior (E).
Fig. 112. Endopod of leg 2, posterior (G).
Fig. 113. Distal margins of endopods in leg 3 of 1 male, posterior (E).
Fig. 114. Leg 5, dorsomesial (D).
Fig. 115. Leg 6, ventral (E).

Hemicyclops diremptus n. sp., female

Fig. 116. Body, dorsal (A).
Fig. 117. Urosome, ventral (C).

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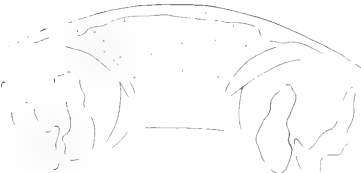
Plate XVII
Hemicyclops diremptus n. sp., female (continued)

Fig. 118. Genital segment, dorsal (H).
Fig. 119. Genital and postgenital segments, lateral (B).
Fig. 120. Area of insertion of a caudal ramus, ventral (I).
Fig. 121. Caudal ramus, dorsal (D).
Fig. 122. Rostral area, ventral (G).
Fig. 123. First antenna, ventral (G).

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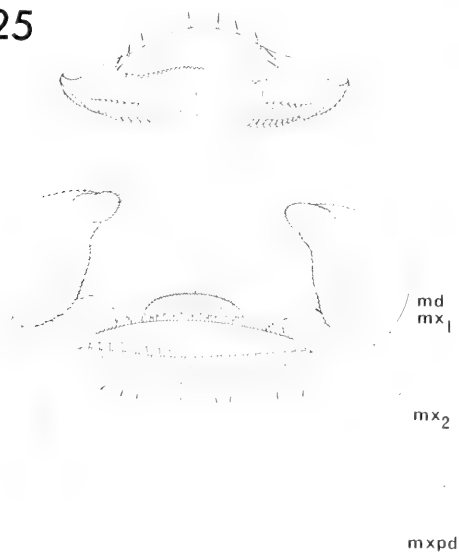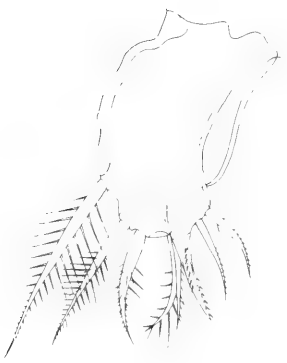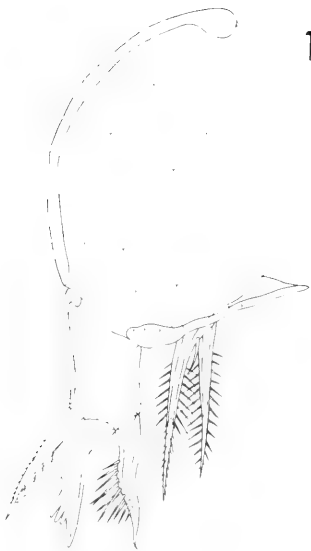
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Plate XVIII
Hemicyclops diremptus n. sp., female (continued)

Fig. 124.   Second antenna, anterior (G).
Fig. 125.   Oral area, ventral (D).
Fig. 126.   Mandible, posterior and ventral (D).
Fig. 127.   Paragnath, posterodorsal (E).
Fig. 128.   First maxilla, posterior (D).
Fig. 129.   Second maxilla, anterior (D).
Fig. 130.   Maxilliped, anterodorsal (G).
Fig. 131.   Tip of maxilliped, posteroventral (E).
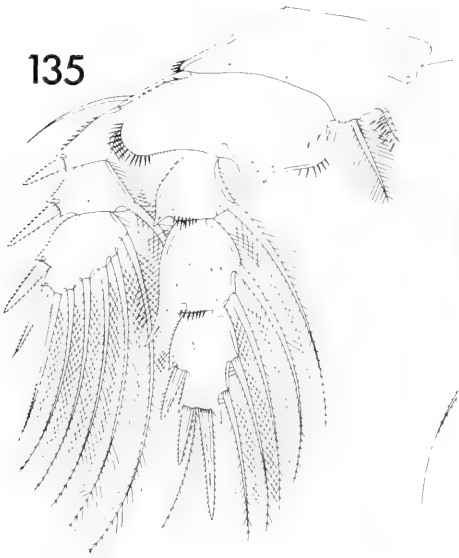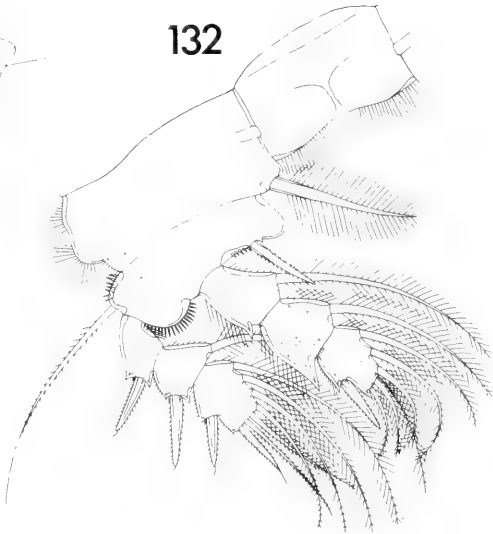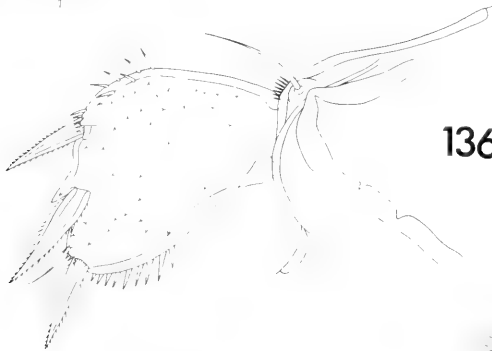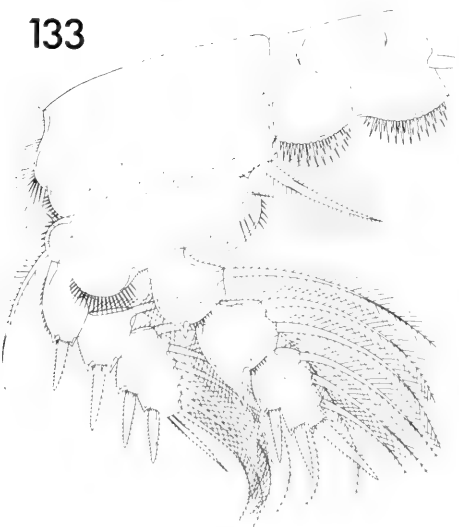
Plate XIX
Hemicyclops diremptus n. sp., female (continued)

Fig. 132. Leg 1, anterior (H).
Fig. 133. Leg 2, anterior (H).
Fig. 134. Leg 3, anterior (H).
Fig. 135. Leg 4, anterior (H).
Fig. 136. Leg 5, dorsal (G).

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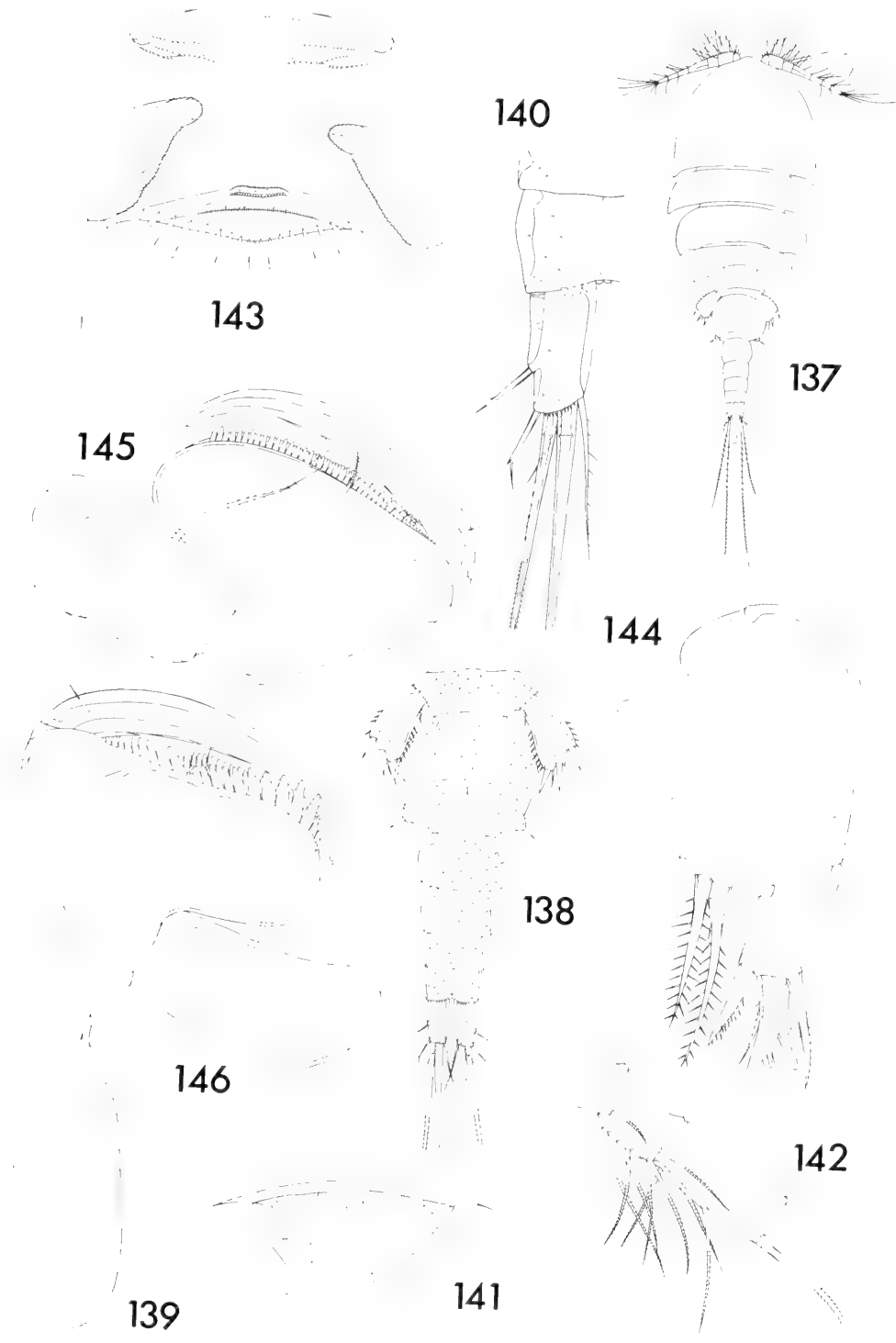
Plate XX
Hemicyclops diremptus n. sp., male

Fig. 137.   Body, dorsal (A).
Fig. 138.   Urosome, ventral (C).
Fig. 139.   Spermatophore from inside body of male (E).
Fig. 140.   Caudal ramus and part of anal segment, ventral (D).
Fig. 141.   Rostral area, ventral (E).
Fig. 142.   Third and fourth segments of first antenna, ventral (D).
Fig. 143.   Oral area, ventral (E).
Fig. 144.   Second maxilla, anterior (E).
Fig. 145.   Maxilliped, anterior (D).
Fig. 146.   Maxilliped, posterior (D).

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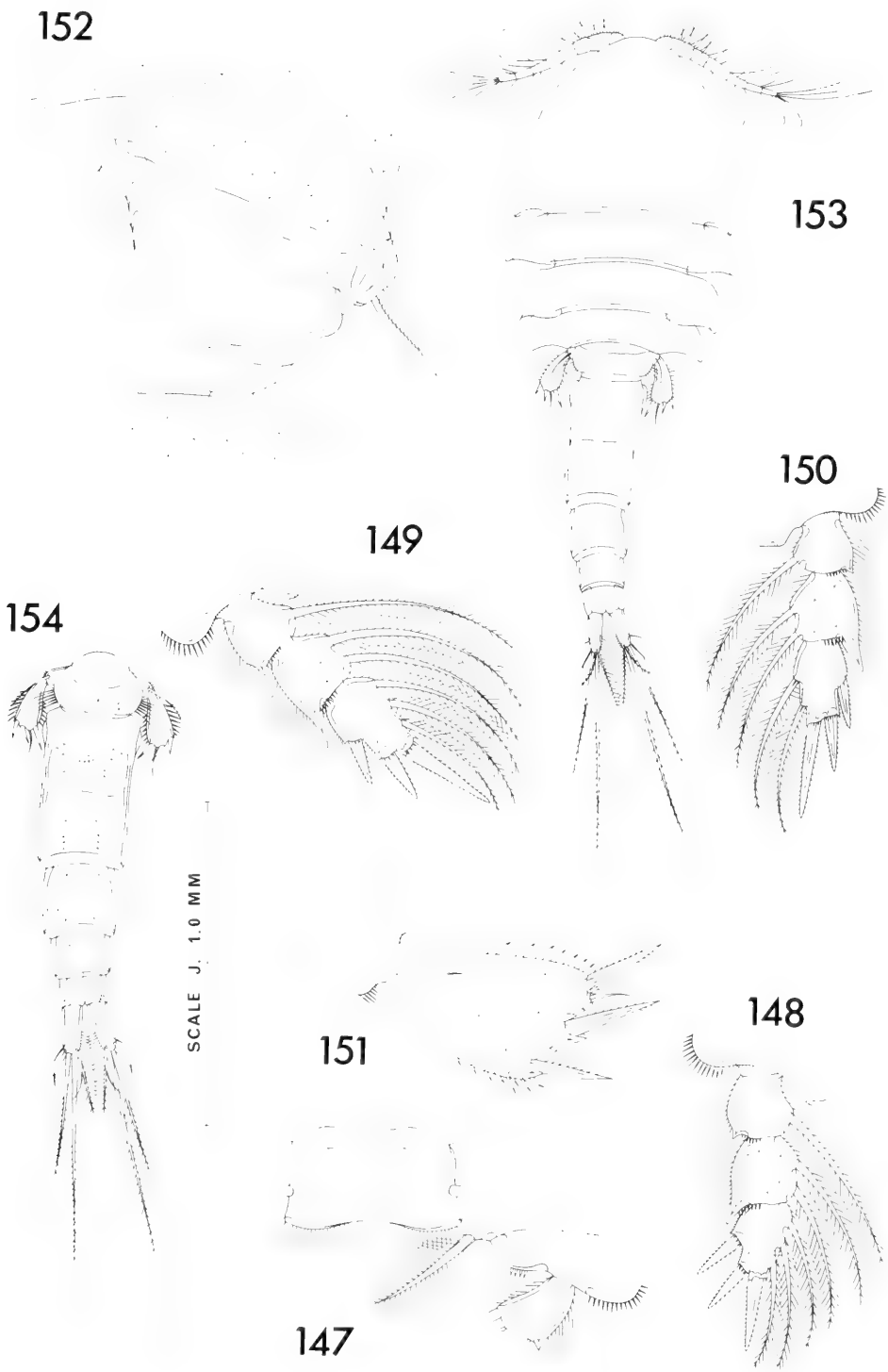
Plate XXI

Hemicyclops diremptus n. sp., male (continued)

Fig. 147.   Portion of leg 1, anterior (G).
Fig. 148.   Endopod of leg 2, anterior (G).
Fig. 149.   Endopod of leg 3, anterior (G).
Fig. 150.   Endopod of leg 4, anterior (G).
Fig. 151.   Leg 5, dorsal (D).
Fig. 152.   Leg 6, ventral (E).

Hemicyclops kombensis n. sp., female

Fig. 153.   Body, dorsal (A).
Fig. 154.   Urosome, dorsal (J).

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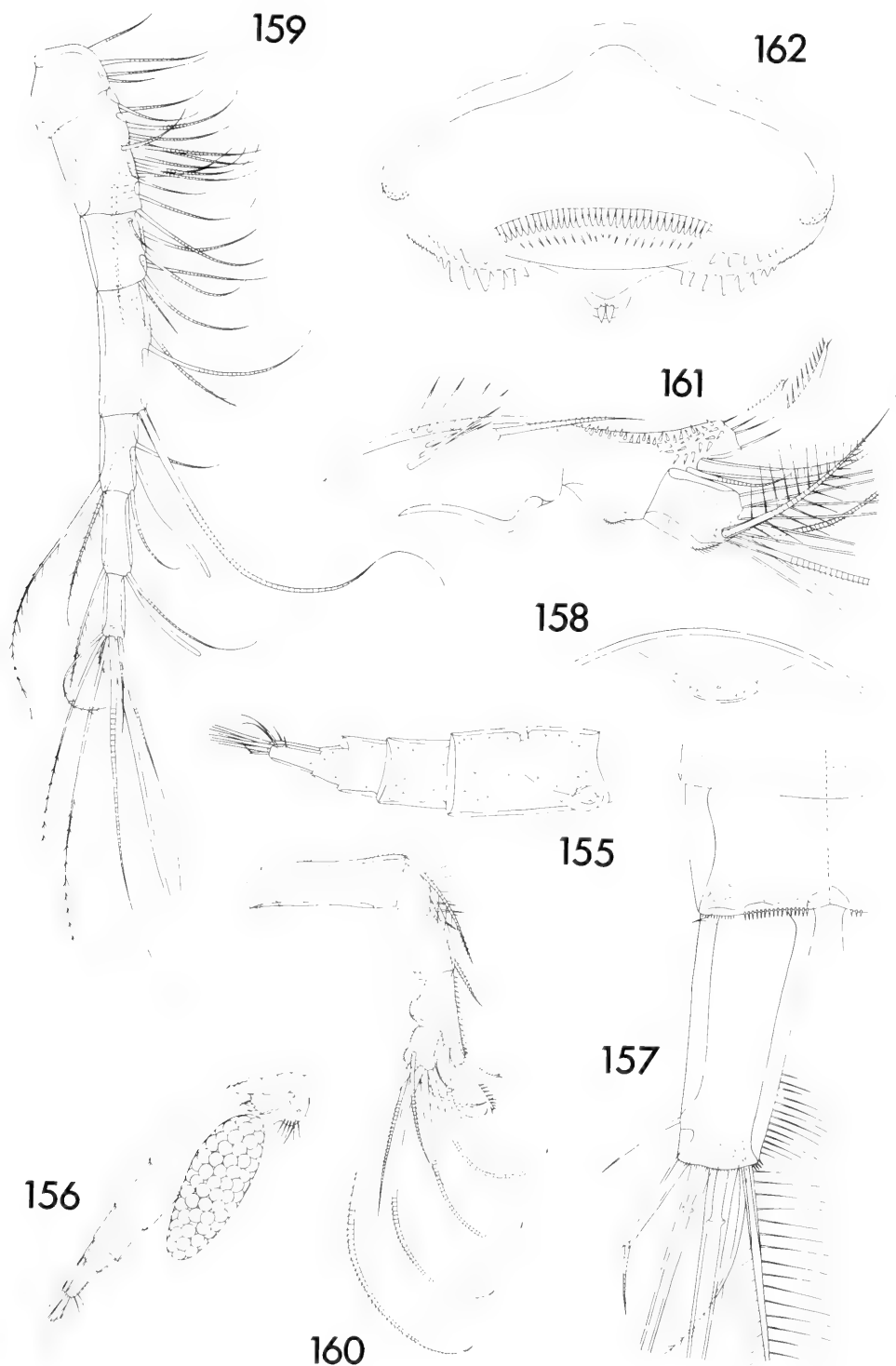
Plate XXII
Hemicyclops kombensis n. sp., female (continued)
Fig. 155.   Genital and postgenital segments, nearly lateral (J).
Fig. 156.   Egg sac attached to urosome, nearly lateral (A).
Fig. 157.   Caudal ramus, ventral (G).
Fig. 158.   Rostral area, ventral (G).
Fig. 159.   First antenna, ventral (H).
Fig. 160.   Second antenna, anterior (H).
Fig. 161.   Last three segments of second antenna, posterior (D).
Fig. 162.   Labrum, ventral and somewhat posterior (E).

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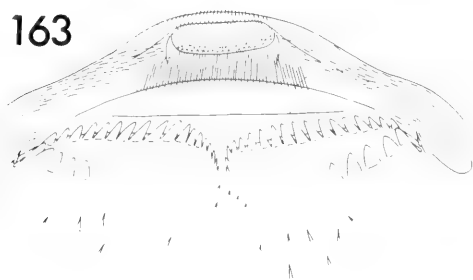
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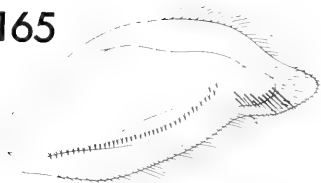
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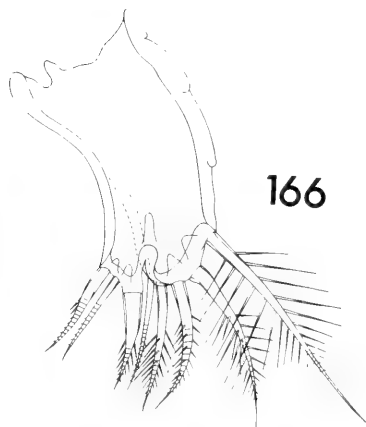
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Plate XXIII
Hemicyclops kombensis n. sp., female (continued)
Fig. 163. Metastomal areas, ventral (E).
Fig. 164. Mandible, anterior and dorsal (D).
Fig. 165. Paragnath, posterior and ventral (E).
Fig. 166. First maxilla, posterior (D).
Fig. 167. Second maxilla, anterior (G).
Fig. 168. Maxilliped, posterior and ventral (G).
Fig. 169. Region between maxillipeds and leg 1, ventral (H).
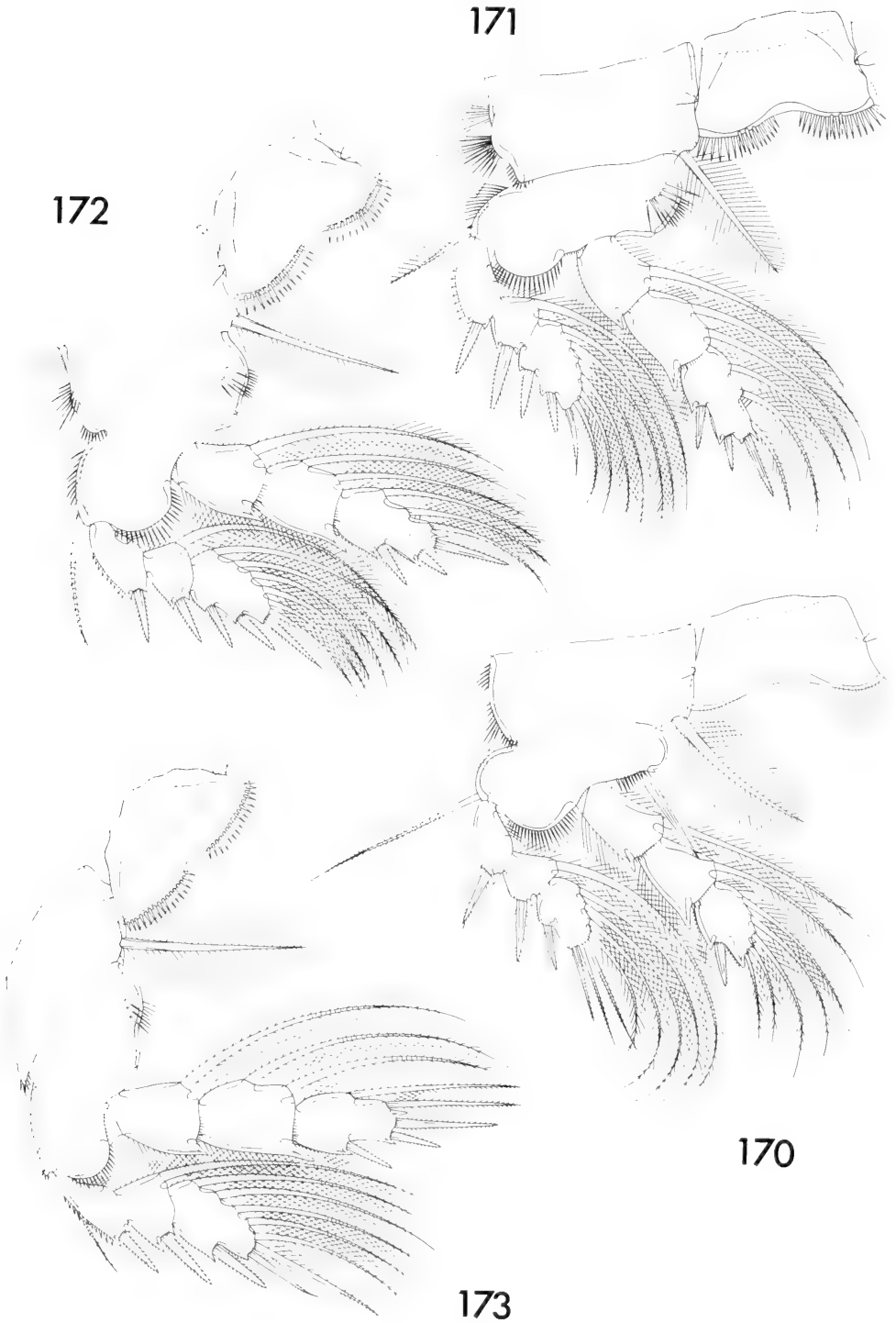
Plate XXIV
Hemicyclops kombensis n. sp., female (continued)

Fig. 170. Leg 1, anterior (H).
Fig. 171. Leg 2, anterior (H).
Fig. 172. Leg 3, anterior (H).
Fig. 173. Leg 4, anterior (H).
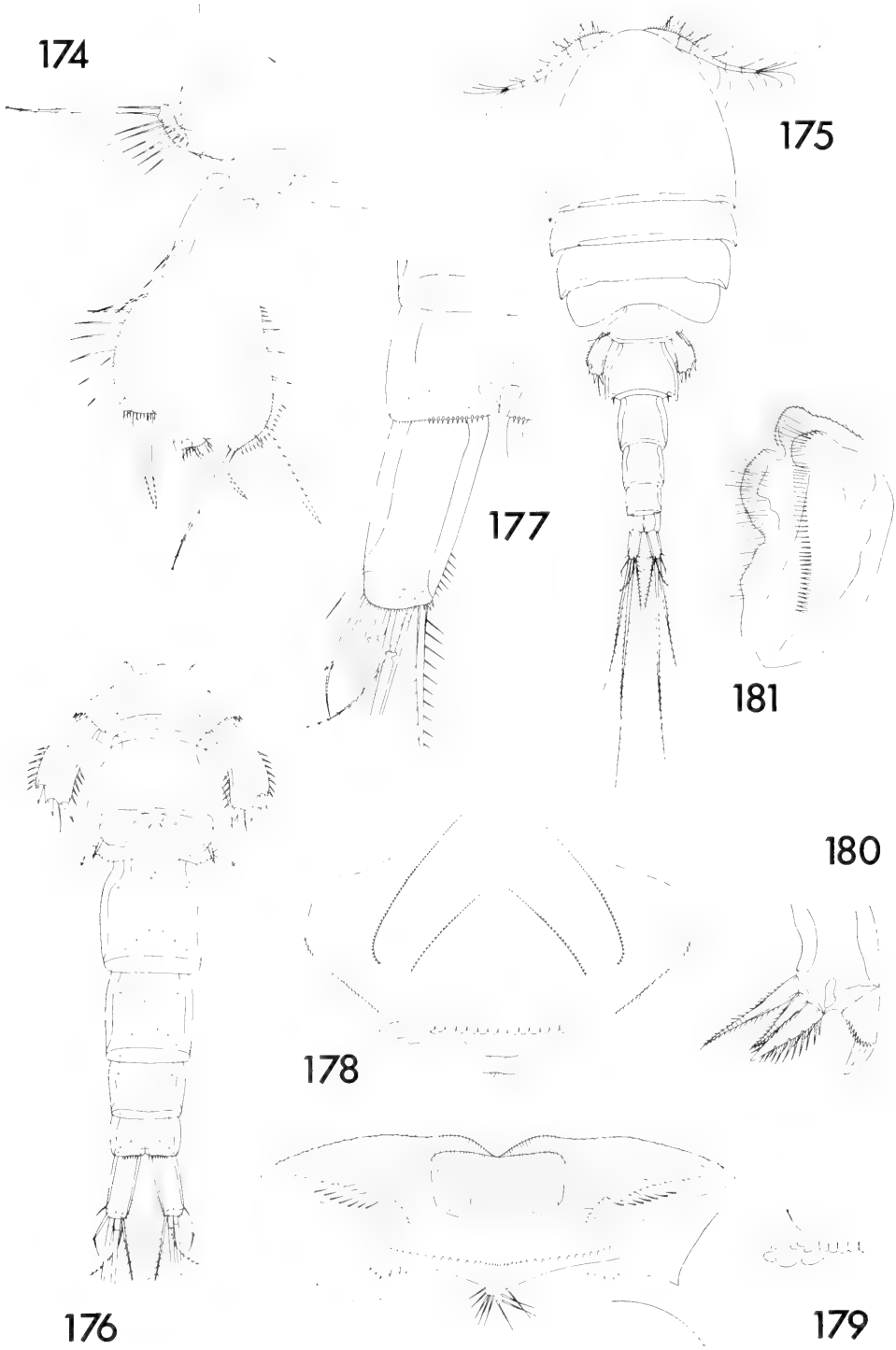
Plate XXV
Hemicyclops kombensis n. sp., female (continued)

Fig. 174. Leg 5, ventral (G).

Hemicyclops kombensis n. sp., male

Fig. 175. Body, dorsal (A).
Fig. 176. Urosome, ventral (C).
Fig. 177. Caudal ramus and part of anal segment, ventral (G).
Fig. 178. Labrum and metastomal areas, ventral (E).
Fig. 179. Spines at corner of labrum, ventral (E).
Fig. 180. Tip of mandible, anterior (D).
Fig. 181. Paragnath, posterior and ventral (E).

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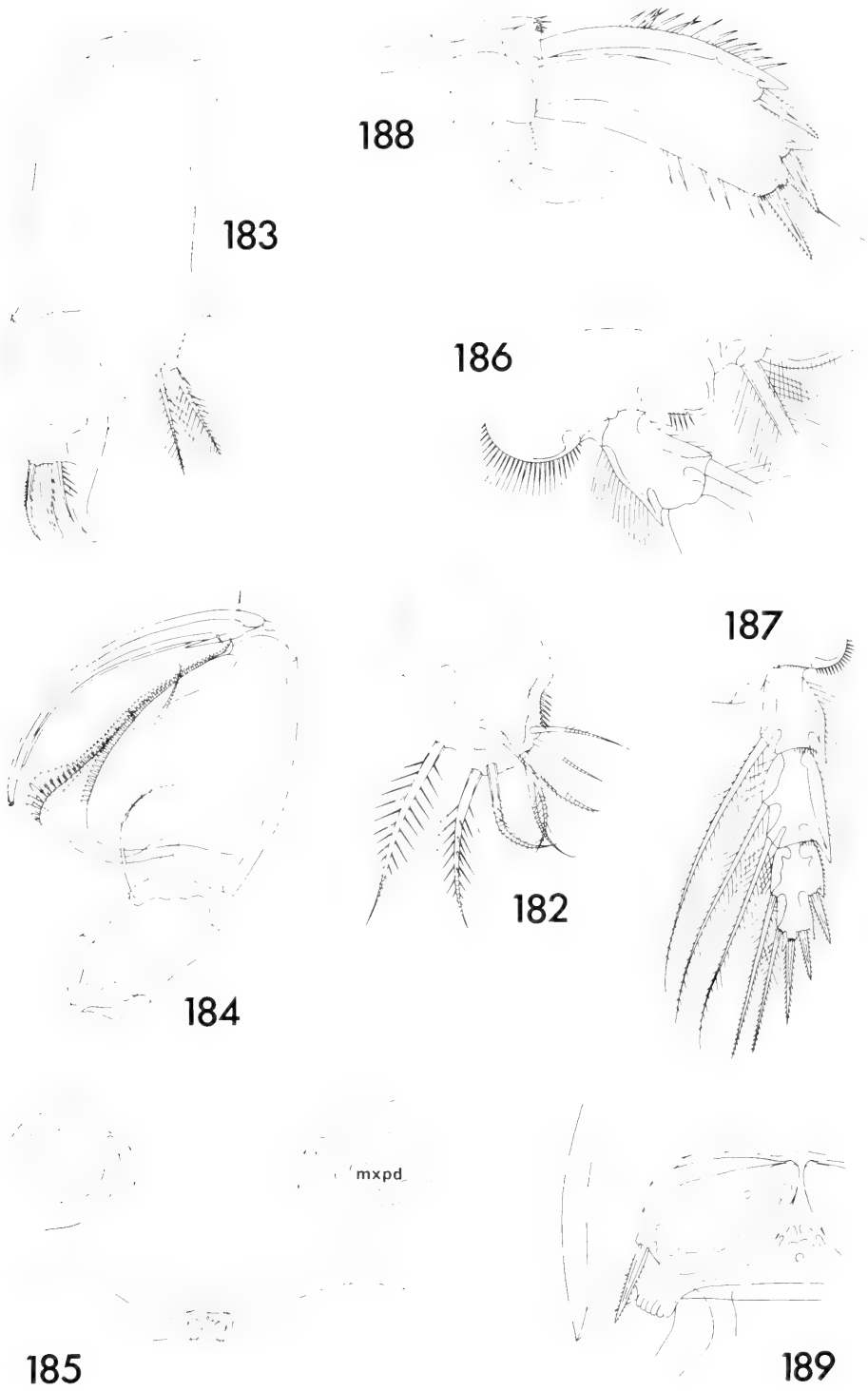
Plate XXVI
Hemicyclops kombensis n. sp., male (continued)

Fig. 182. First maxilla, posterior (D).
Fig. 183. Second maxilla, anterior (G).
Fig. 184. Maxilliped, anterior (H).
Fig. 185. Region between maxillipeds and leg 1, ventral (H).
Fig. 186. Detail of leg 1, anterior (G).
Fig. 187. Endopod of leg 4, anterior (H).
Fig. 188. Leg 5, dorsal (G).
Fig. 189. Leg 6, ventral (G).
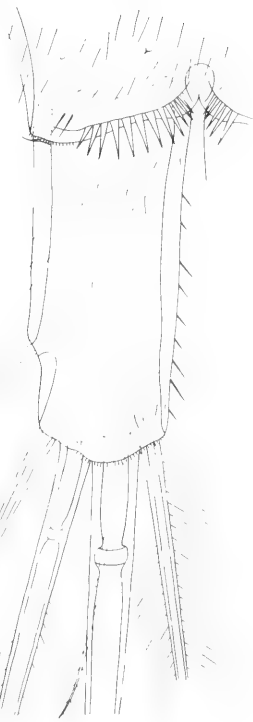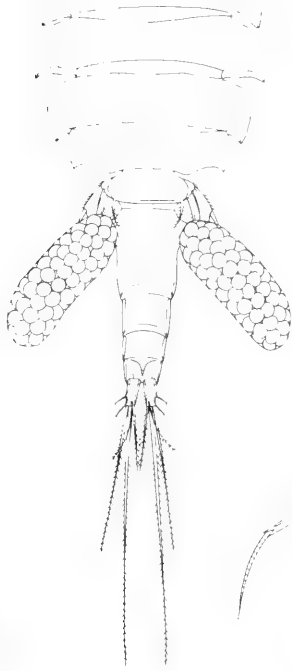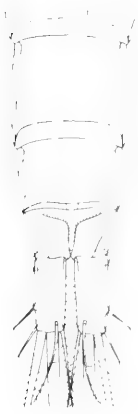
Plate XXVII
Hemicyclops biflagellatus n. sp., female

Fig. 190. Body, dorsal (J).
Fig. 191. Urosome, dorsal (B).
Fig. 192. Area of attachment of egg sac, dorsal (E).
Fig. 193. Caudal ramus, ventral (E).
Fig. 194. Rostral area, ventral (E).
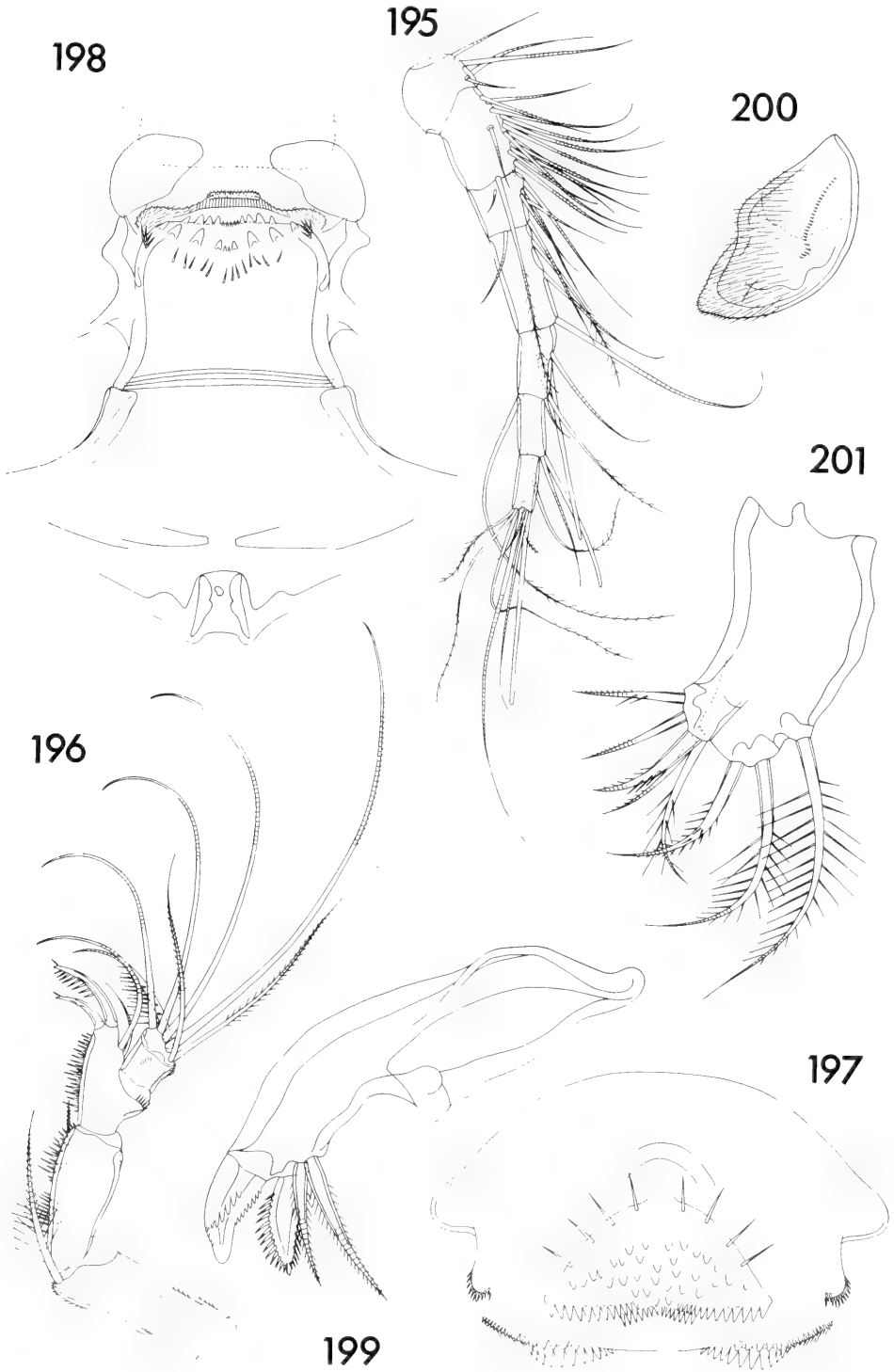
Plate XXVIII
Hemicyclops biflagellatus n. sp., female (continued)

Fig. 195. First antenna, anterodorsal (H).
Fig. 196. Second antenna, anterior (G).
Fig. 197. Labrum, ventral (E).
Fig. 198. Metastomal areas and region between maxillipeds and leg 1 (with outline of labrum in dashed lines), ventral (G).
Fig. 199. Mandible, anterior and dorsal (E).
Fig. 200. Paragnath, posterior (E).
Fig. 201. First maxilla, posterior (E).
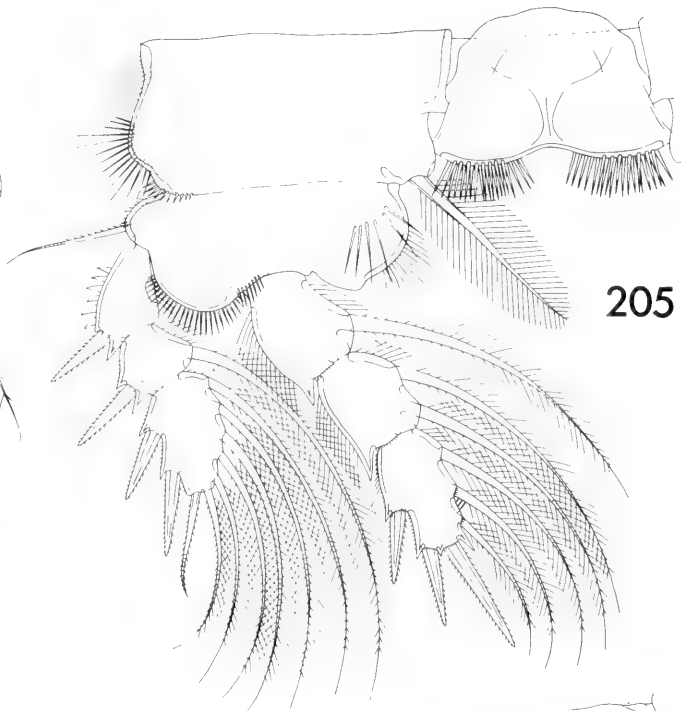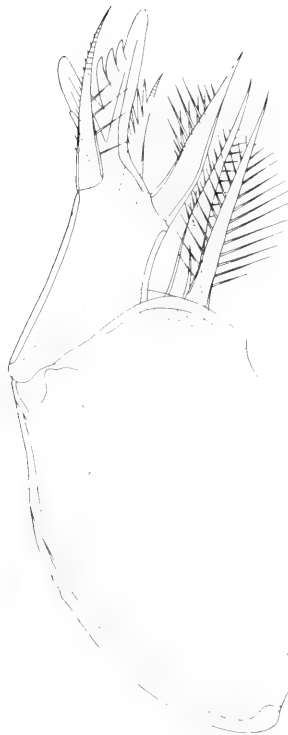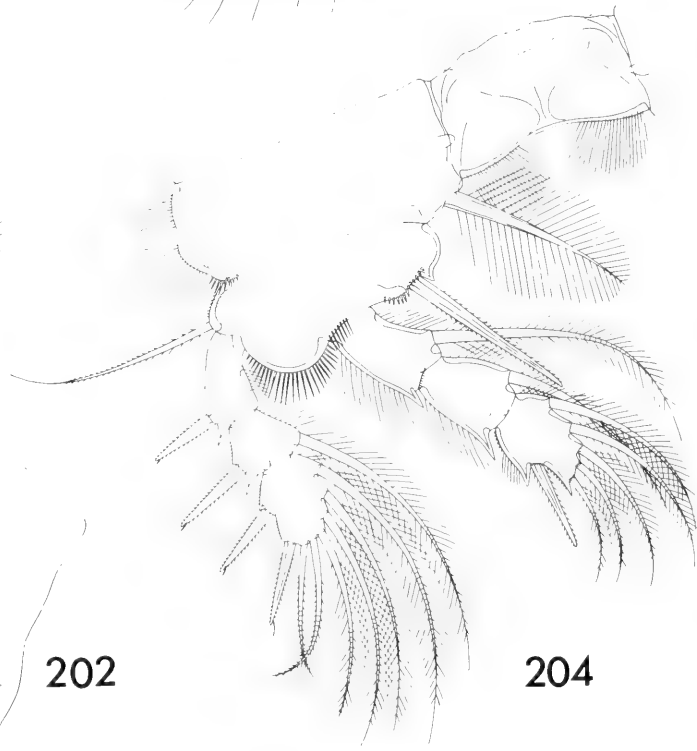
Plate XXIX
Hemicyclops biflagellatus n. sp., female (continued)
Fig. 202.   Second maxilla, anterior (E).
Fig. 203.   Maxilliped, dorsal (D).
Fig. 204.   Leg 1, anterior (G).
Fig. 205.   Leg 2, anterior (G).
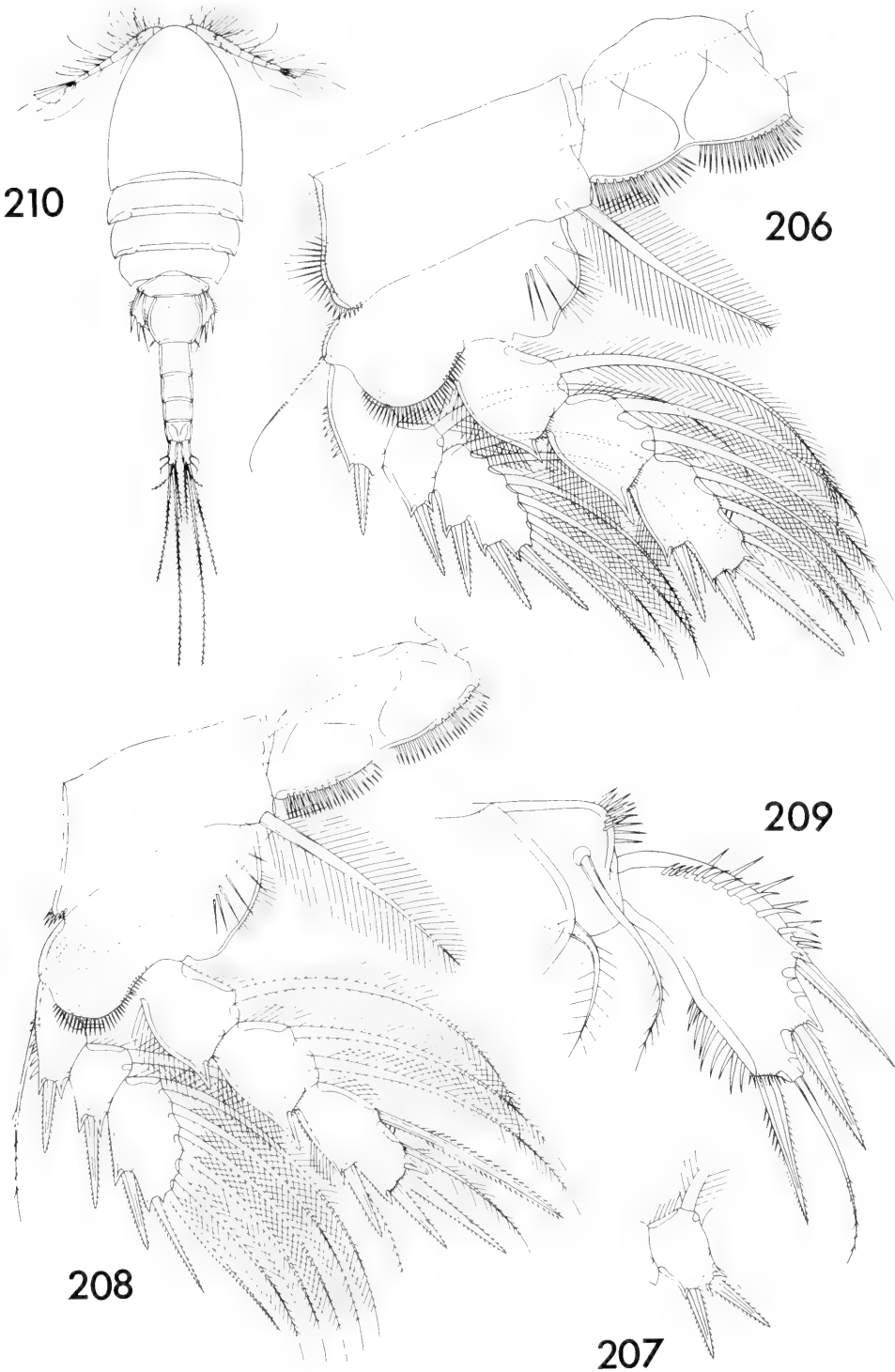
Plate XXX
Hemicyclops biflagellatus n. sp., female (continued)
Fig. 206. Leg 3, anterior (G).
Fig. 207. Abnormal second segment of exopod of leg 3, anterior (G).
Fig. 208. Leg 4, anterior (G).
Fig. 209. Leg 5, dorsal (D).
Hemicyclops biflagellatus n. sp., male
Fig. 210. Body, dorsal (J).

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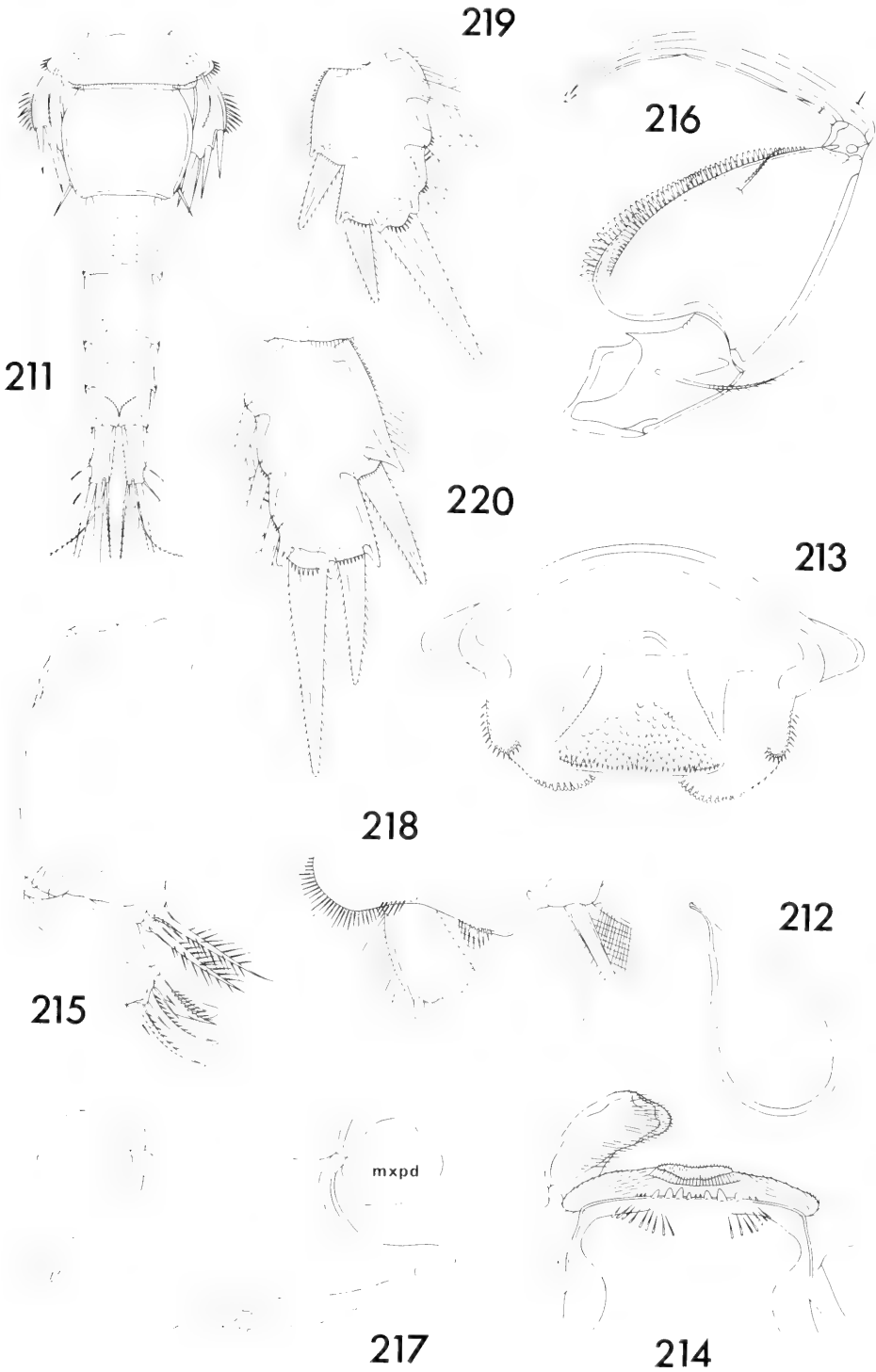
Plate XXXI
Hemicyclops biflagellatus n. sp., male (continued)

Fig. 211. Urosome, dorsal (B).
Fig. 212. Spermatophore attached to female, ventral (E).
Fig. 213. Labrum, ventral (E).
Fig. 214. Metastomal areas, with one paragnath in position, ventral (D).
Fig. 215. Second maxilla, anterior (D).
Fig. 216. Maxilliped, anterior (G).
Fig. 217. Region between maxillipeds and leg 1, ventral (G).
Fig. 218. Detail of leg 1, anterior (D).
Fig. 219. Last segment of endopod of leg 2, anterior (E).
Fig. 220. Last segment of endopod of leg 3, anterior (E).
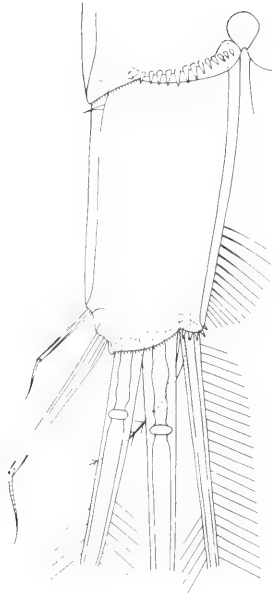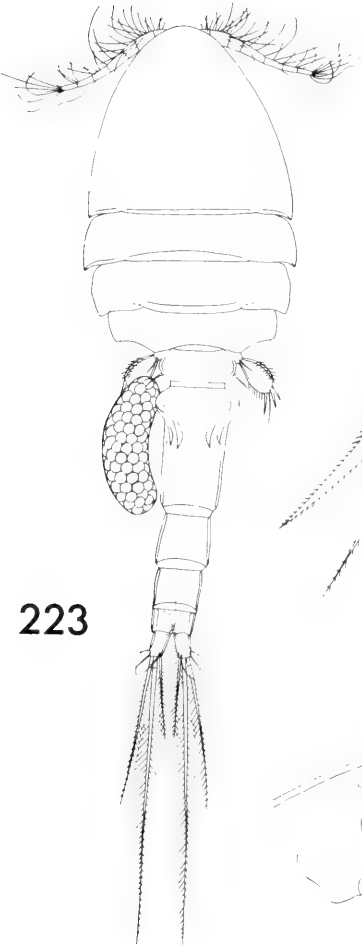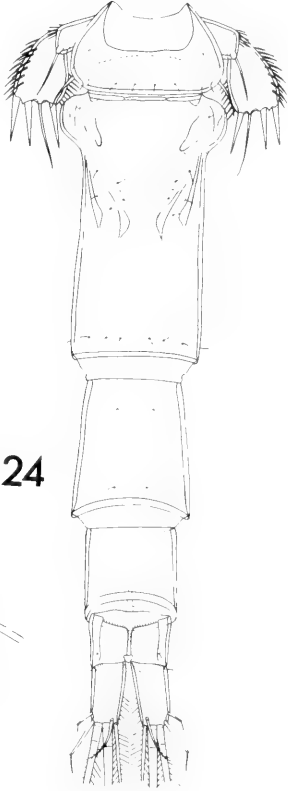
Plate XXXII
Hemicyclops biflagellatus n. sp., male (continued)
Fig. 221.   Leg 5, dorsal (D).
Fig. 222.   Leg 6, ventral (D).

Hemicyclops acanthosquillae n. sp., female
Fig. 223.   Body, dorsal (A).
Fig. 224.   Urosome, dorsal (C).
Fig. 225.   Portion of segment of leg 5 showing setiform process, dorsal (D).
Fig. 226.   Caudal ramus, ventral (D).
Fig. 227.   Rostral area, ventral (G).

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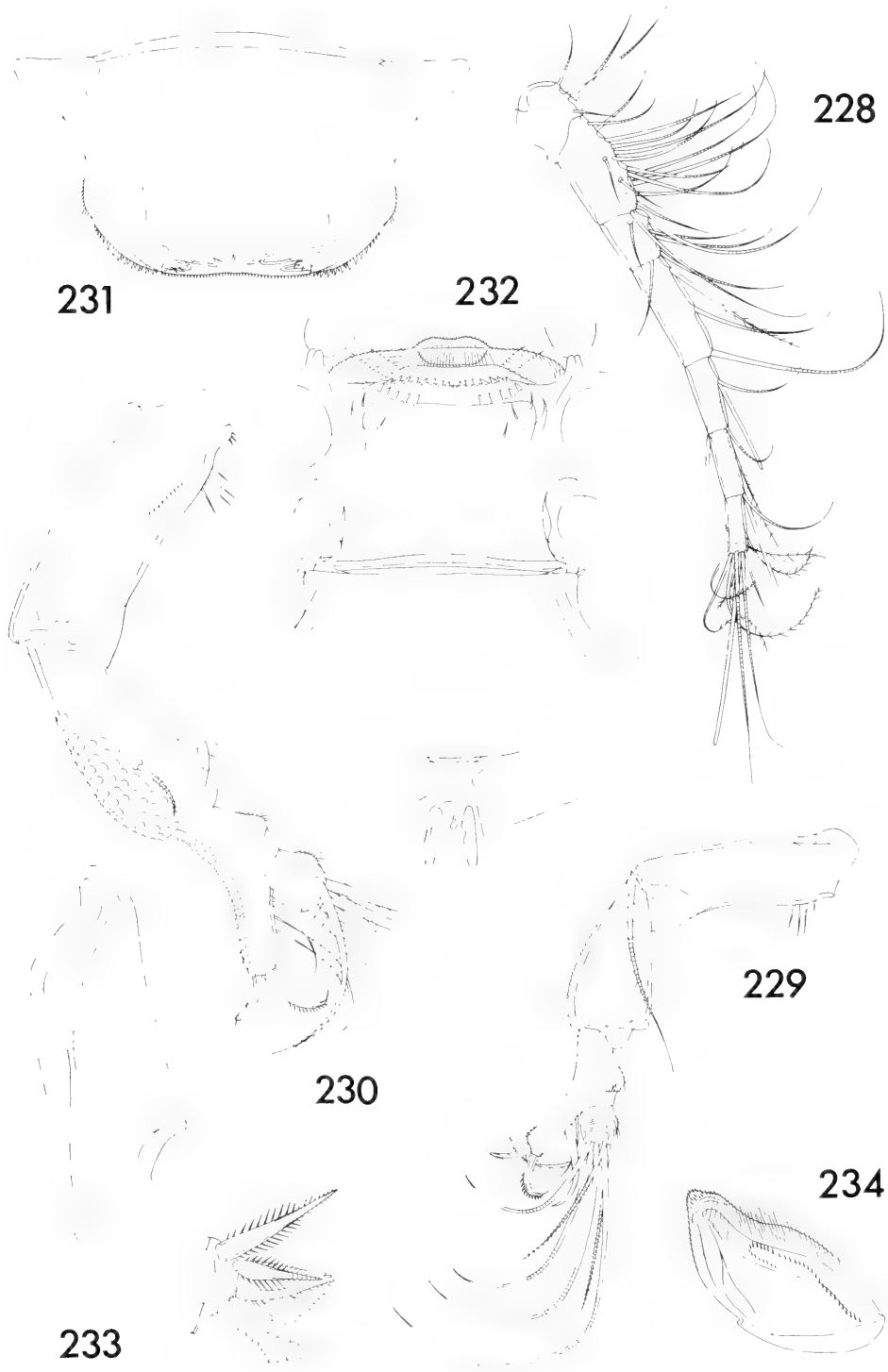
Plate XXXIII
Hemicyclops acanthosquillae n. sp., female (continued)

Fig. 228. First antenna, anterodorsal (H).
Fig. 229. Second antenna, anterior (G).
Fig. 230. Second antenna, posterior (D).
Fig. 231. Labrum, ventral (D).
Fig. 232. Metastomal areas and region between maxillipeds and leg 1, ventral (G).
Fig. 233. Mandible, anterior and dorsal (E).
Fig. 234. Paragnath, posterior and ventral (E).
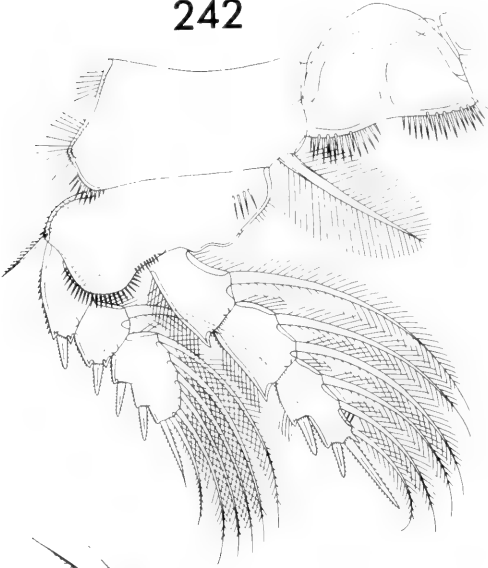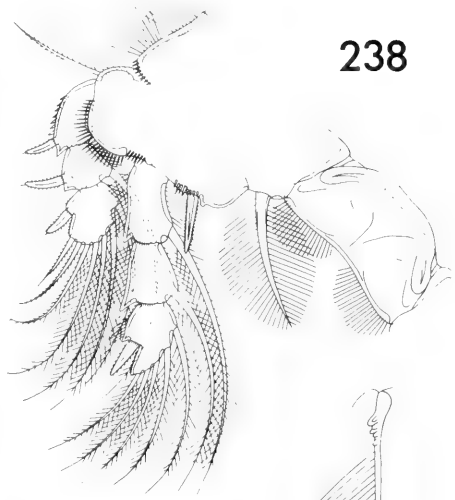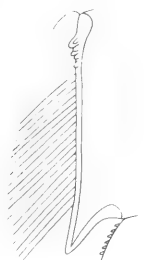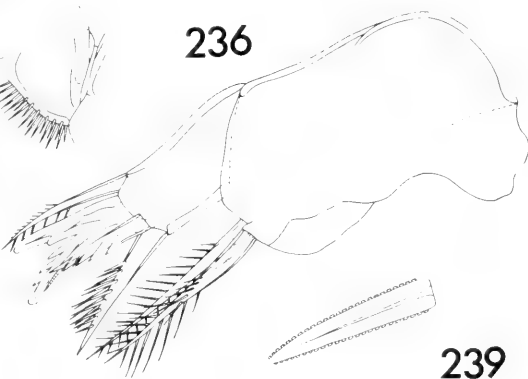
Plate XXXIV
Hemicyclops acanthosquillae n. sp., female (continued)

Fig. 235. First maxilla, posterior (E).
Fig. 236. Second maxilla, posterior (D).
Fig. 237. Maxilliped, dorsal (D).
Fig. 238. Leg 1, anterior (H).
Fig. 239. Inner spine on basis of leg 1, anterior (E).
Fig. 240. Leg 2, anterior (H).
Fig. 241. Outer edge of second segment of endopod of leg 2, anterior (E).
Fig. 242. Leg 3, anterior (H).
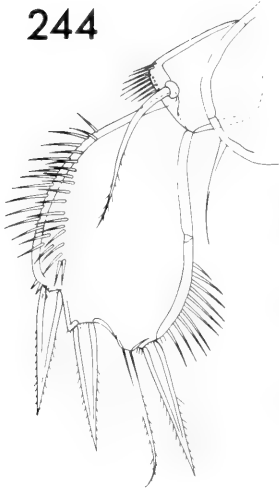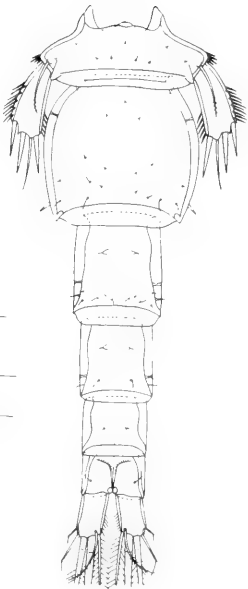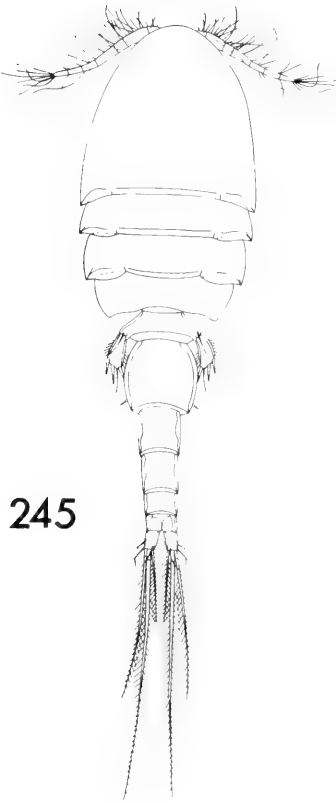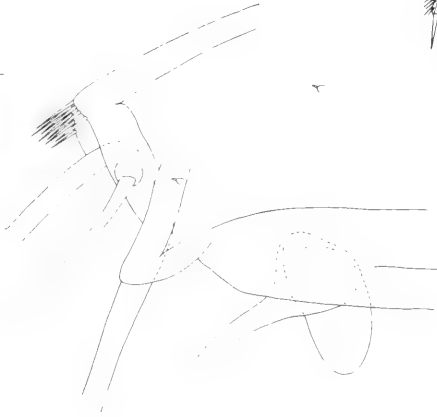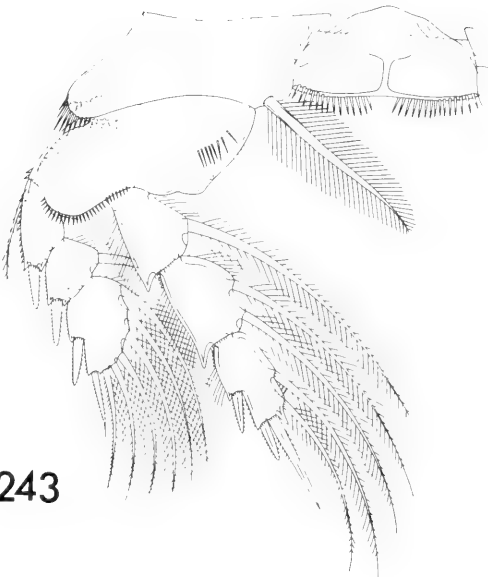
Plate XXXV
Hemicyclops acanthosquillae n. sp., female (continued)
Fig. 243. Leg 4, anterior (H).
Fig. 244. Leg 5, dorsal (G).

Hemicyclops acanthosquillae n. sp., male
Fig. 245. Body, dorsal (A).
Fig. 246. Urosome, dorsal (C).
Fig. 247. Portion of segment of leg 5 showing projection, dorsal (E).
Fig. 248. Spermatophore (G).

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New Oceanic Cheilodipterid Fishes
from the Indian Ocean

by GILES W. MEAD and J. E. De FALLA

Museum of Comparative Zoology, Harvard University

NEW OCEANIC CHEILODIPTERID FISHES FROM THE INDIAN OCEAN

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ABSTRACT

The collections made in or adjacent to the Indian Ocean during voyages of R/V *Anton Bruun* and the "Monsoon" Expedition of Scripps Institution of Oceanography include six species of high-seas cheilodipterid fishes. Two, *Rosenblattia robusta* and *Florenciella lugubris*, are described here as new genera and species; the other four, *Howella brodiei*, *Bathysphyraenops simplex*, *Brinkmannella elongata*, and a second unidentified species of *Brinkmannella* are new records for the Indian Ocean. Included in the description of *Rosenblattia robusta* is material taken in the sub-Antarctic part of the Pacific Ocean during the Antarctic Research Program of the University of Southern California.

INTRODUCTION

In addition to the abundant mesopelagic malacopterygians such as myctophids and gonostomatids, midwater nets fished far from shore occasionally take spiny-rayed fishes which are related to coastal groups. We are concerned here with one such group, the midwater segment of the percomorph family Cheilodipteridae (Apogonidae), a family that is chiefly coastal, but that does contain a few off-shore species.

Although these fishes are customarily referred to the Cheilodipteridae, the family relationships have not properly been established. For example, Norman (1957:242A)

tentatively placed the genera *Howella*, *Neoscombrops*, *Bathysphyraenops*, and *Apogonops* in the serranid subfamily Serraninae. The problem is the recognition of those characters which are adaptations for mesopelagic life as distinct or partially distinct from those which reflect ancestry and relationship to an inshore family or subfamily. Various features found in these fishes, such as reduction or loss of color pattern, lack of countershading, occasional presence of terminal and horizontal antrorse teeth in the jaws, increased development of the lateral line, etc., are certainly characteristic of many mesopelagic fishes of diverse relationships. Variability in other characters, such as number of anal spines, deciduous *vs.* adherent scales, presence or absence of opercular spines, and the extension of the lateral line onto the caudal fin, suggests that the group is not homogeneous. However, some of these features also may reflect the requirements of oceanic life as well as ancestry. A critical study of the family relationships is clearly in order, but cannot be attempted here.

The midwater species discussed below are so different from their coastal relatives that comparison is pointless. However, mindful of the possibility that these forms may represent the pelagic young or prejuveniles of benthic cheilodipterids from the continental shelf and abyssal plain, various benthic genera (e.g. *Brephostoma* Alcock, *Synagrops* Günther, *Epigonus* Rafinesque, *Neoscombrops* Gilchrist, *Paroncheilus*

Smith) were considered while arriving at the identifications which are given.

Only two oceanic cheilodipterids, *Oxyodon macrops* Brauer 1906 and *Hynnodus atherinoides* Gilbert, 1905 (Fourmanoir, 1957) have been previously reported from the Indian Ocean. Neither of these is represented in our collections.

The area with which we are primarily concerned is the Indian Ocean. The type locality of *Rosenblattia robusta* lies in the southwestern Pacific, but the species was also caught in the Indian Ocean. In addition, we have included in our description of this species a few specimens taken in the sub-Antarctic part of the Pacific Ocean. Our principal material was taken during Cruises III and VI of R/V *Anton Bruun* during the American Program in Biology, International Indian Ocean Expedition. Cruise III fished along the 60°E meridian from 12°N to 44°S, 13 August to 13 September, 1963. Cruise VI sampled waters along 65°E from 18°N to 41°S, 17 May to 4 July, 1964. Supplementing the *Anton Bruun* collections are several lots taken by Scripps Institution of Oceanography during its "Monsoon" Expedition to the Pacific and Indian Oceans, October, 1960 to March, 1961 (Clarke, 1963), and a few lots taken by the R/V *Eltanin* during the Antarctic Research Program of the University of Southern California.

Both cruises of the *Anton Bruun* used a 10-foot Isaacs-Kidd Midwater Trawl; the Foxton Trousers (see Foxton, 1963), an opening-closing device designed to separate a shallow from a deep fraction of the trawl haul; and occasionally a time-depth recorder. Attempts to calibrate the Foxton Trousers by repeated lowerings of the instrument on the hydrographic wire showed that the depth at which the device triggered varied greatly. The device did separate the shallow from the deep part of the catch, but the actual depth of such separation was imprecise. Even limits of error of half or double the nominal depth of separation may be unrealistically narrow.

Our methods of counting and measuring are chiefly those of Hubbs and Lagler (1947). The tip of the snout is taken as the midpoint of the upper jaw, even though this point may not be terminal. The length of the head is taken from the tip of the snout to the most posterior edge of the gill flap exclusive of opercular spines. The number of scales between the first dorsal fin and the lateral line is counted along the oblique row beginning at the base of the second dorsal spine. This count includes the small scale at the base of the fin but excludes the lateral line scale. The count between the lateral line and anal fin is made on the oblique row terminating at the base of the first anal spine. This count also excludes the lateral line scale, and is somewhat variable due to the occasional presence of a half scale at either end of the row. The last soft dorsal and the last anal rays may or may not be divided to the base, but in either instance the ray is counted as one.

The following abbreviations are used: IIOE (International Indian Ocean Expedition), IKMT (Isaacs-Kidd Midwater Trawl), l.s.t. (local standard time), t.d.r. (time-depth recorder), s.l. (standard length), ANSP (Academy of Natural Sciences of Philadelphia), LACM (Los Angeles County Museum), MCZ (Museum of Comparative Zoology, Harvard University), SIO (Scripps Institution of Oceanography), USC (University of Southern California), and USNM (United States National Museum).

gram of which the *Anton Bruun* cruises were a part. This study was aided by Grant GF147 from the National Science Foundation to Harvard University, whose support is here gratefully acknowledged.

ROSENBLATTIA, NEW GENUS

Type species: Rosenblattia robusta new species. Gender of generic name: feminine.

Generic characters. Rosenblattia is distinguished from all other known oceanic cheilodipterid fishes by the more robust body and by the pair of caudal keels formed by the scales of the mid-lateral series of the caudal peduncle. The high number (*ca.* 52) of scales in the lateral line and the antrorse teeth anteriorly in both jaws distinguish this genus from all others except *Florenciella* which is discussed below.

All scales strongly ctenoid; head almost completely covered, fins largely naked. Scales on body small and numerous; about four between base of dorsal fin and lateral line and about fifteen between lateral line and base of anal fin. Lateral line complete, uninterrupted, and continuing onto caudal fin, the scales along the caudal peduncle particularly spinulose and V-shaped. Strong spines in vertical fins. Anal fin with two spines. Body raised and stiffened at origins of unpaired fins. Procurrent caudal fin rays stiff and spiny, their tips free. Eye large, a small aphakic space present. A few discrete simple spines along the upper edge of opercle; opercle and subopercle elsewhere serrated. Upper edge of orbit spiny when viewed from above. Teeth present on jaws, vomer, and palatines; some of anterior jaw teeth antrorse.

This genus is named in honor of Dr. Richard Rosenblatt of Scripps Institution of Oceanography, friend and fellow ichthyologist.

ROSENBLATTIA ROBUSTA, NEW SPECIES

Holotype. An 84.8 mm s.l. specimen taken in the South Pacific by the Scripps Institution of Oceanography "Monsoon" Expedition; IKMT haul no. 17; 28 February to 1 March, 1961; 2206 to 0250 hrs. l.s.t.; 46° 53′S, 179°48′W to 46°42′S, 179°32′W; maximum calculated depth 1878 m, open net. SIO 61–45.

Paratypes. Two, 94.4 and 48.8 mm s.l.; same data as holotype. MCZ and SIO, respectively.

One, 75.8 mm s.l.; R/V *Eltanin*, USC Antarctic Research Program, Cruise 11; Sta. 882; 30 December 1963; 0805 to 1210 hrs. l.s.t.; 55°10′S, 114°15′W to 55°52′S, 114° 22′W; IKMT; maximum depth of sampling 1737 m, open net. LACM 10075.

One, 67.0 mm s.l.; R/V *Eltanin*, USC Antarctic Research Program, Cruise 10; Sta. 846; 10 November 1963; 2315 to 0330 hrs. l.s.t.; 57°52′S, 74°43′W to 57°27′S, 74°42′W; IKMT; maximum depth of sampling 1829 m, open net. LACM 10074.

One, 61.0 mm s.l.; R/V *Eltanin*, USC Antarctic Research Program, Cruise 13; Sta. 1107; 24 May 1964; 0513 to 0855 hrs. l.s.t.; 57°59.6′S, 90°36.3′W to 58°20′S, 90°46.9′W; IKMT; maximum depth of sampling 713 m, open net. LACM 10077.

One, 49.9 mm s.l.; R/V *Eltanin*, USC Antarctic Research Program, Cruise 13; Sta. 1099; 22 May 1964; 1510 to 1845 hrs. l.s.t.; 56°59.9′S, 89°09.3′W to 57°03.1′S, 88°54.3′ W; IKMT; maximum depth of sampling 759 to 1207 m, open net. LACM 10076.

One, 49.5 mm s.l.; R/V *Eltanin*, USC Antarctic Research Program, Cruise 15; Sta. 1380; 17–18 November 1964; 2250 to 0250 hrs. l.s.t.; 54°01′S, 145°02′W to 53°53′S, 145°13′W; IKMT; maximum depth of sampling 841 m, open net. LACM 10078.

One, 49.0 mm s.l.; R/V *Eltanin*, USC Antarctic Research Program, Cruise 6; Sta. 348; 4 December 1962; 1125 to 1445 hrs. l.s.t.; 54°40.1′S, 58°57.8′W to 55°05.8′S, 59°05.3′ W; IKMT; maximum depth of sampling 896 m, open net. LACM 10073.

One, 35.1 mm s.l.; "Monsoon" Expedition; IKMT haul no. 13; 13 January 1961; 0004 to 0457 hrs. l.s.t.; 49°26′30″S, 132° 18′24″E to 49°21′00″S, 132°39′24″E; maximum calculated depth 1878 m, open net. SIO 61–41.
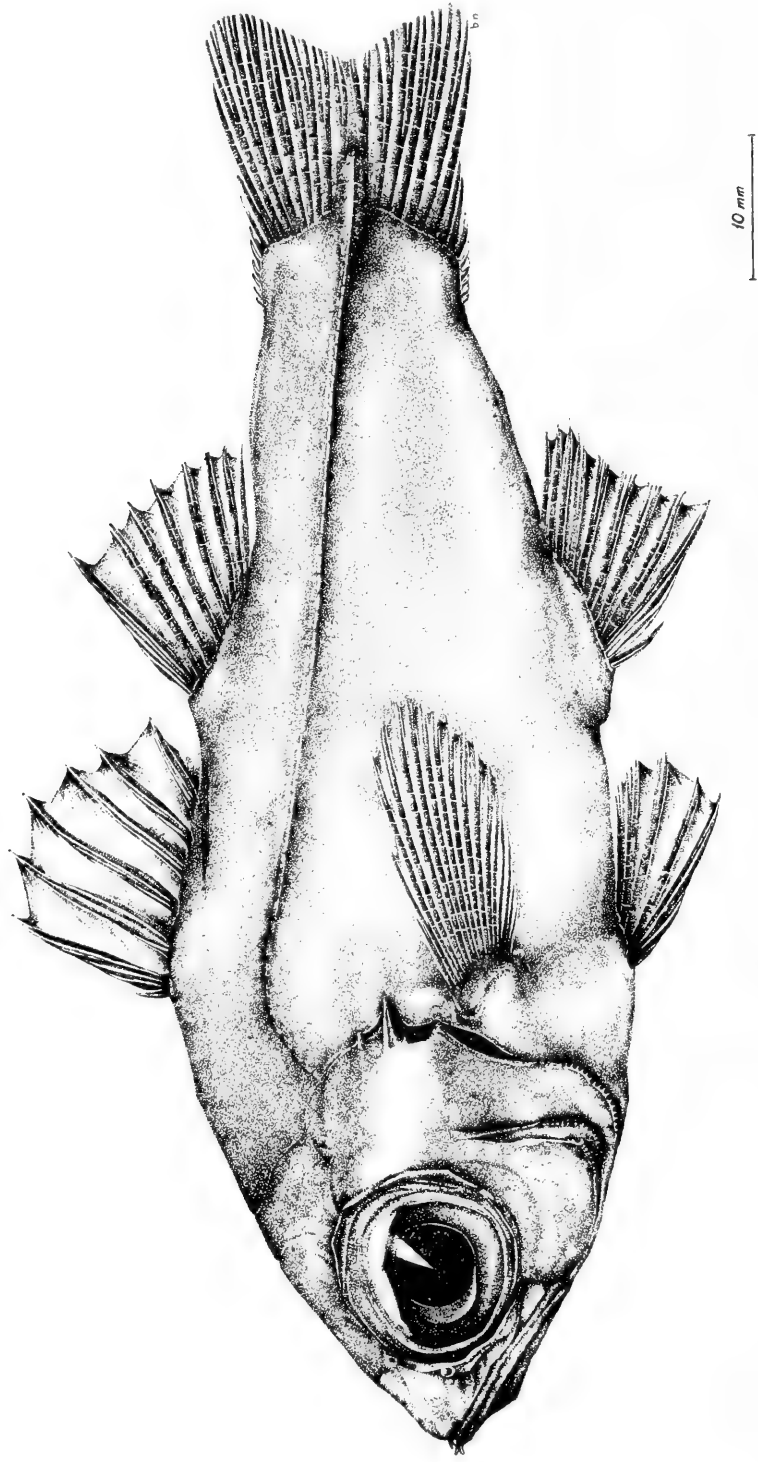
Figure 1. *Rosenblattia robusta*, new genus and species; holotype, 84.8 mm in standard length; SIO 61-45. Squamation not shown. Drawn by Basil G. Nafpaktitis.

Table 1. Proportional dimensions (in per cent of standard length) of nine specimens, including the holotype, of *Rosenblattia robusta*

	SIO 61-45	Holotype SIO 61-45	LACM 10075	LACM 10074	LACM 10077	LACM 10076	LACM 10073	SIO 61-45	SIO 61-41
Standard length (mm)	94.4	84.8	75.8	67.0	61.0	49.9	49.0	48.8	35.1
Fork length	112.0	113.1	111.2	110.6	115.1	114.2	112.4	111.2	118.2
Greatest depth of body	36.8	38.0	38.7	38.7	40.0	38.5	39.8	42.0	39.9
Least depth of caudal peduncle	16.2	17.3	15.0	14.9	14.9	13.6	14.7	14.5	14.0
Greatest width of body	23.3	23.6	22.3	24.2	26.4	24.0	25.1	25.0	27.4
Snout to origin of first dorsal fin	40.8	40.8	39.6	43.7	41.0	42.1	43.3	45.5	48.7
Snout to origin of anal fin	67.3	64.4	67.7	65.8	73.1	72.1	71.6	68.0	72.4
Snout to insertion of ventral fin	41.7	40.3	47.9	41.8	50.0	47.7	47.8	46.3	47.6
Snout to insertion of pectoral fin	36.7	36.0	38.4	37.0	41.0	39.3	40.4	41.0	43.9
Length of base of first dorsal fin	17.8	17.1	16.2	14.5	14.9	14.6	15.9	14.7	14.2
Length of base of second dorsal fin	11.6	11.2	11.2	10.9	10.5	13.0	11.8	10.6	11.7
Distance between first and second dorsal fins	7.6	8.1	7.7	7.5	7.4	8.2	7.1	7.4	7.4
Distance between anus and insertion of ventral fin	19.6	18.6	16.2	19.3	18.4	21.8	19.0	20.5	18.5
Distance between anus and origin of anal fin	5.9	6.1	4.4	4.9	5.1	5.2	5.3	5.5	8.3
Length of pectoral fin	24.9	24.8	25.7	27.6	26.7	28.7	28.6	28.7	29.9
Length of ventral fin	16.9	18.9	19.5	21.6	20.3	20.0	20.8	19.5	21.7
Length of head	35.5	35.1	34.7	36.3	38.0	37.3	39.0	38.9	42.2
Length of snout	8.5	7.9	8.6	8.1	8.7	7.6	8.4	8.4	8.8
Length of upper jaw	14.9	15.9	15.6	16.7	17.7	18.0	17.6	18.2	20.8
Horizontal diameter of eye	13.3	15.0	14.5	15.7	17.5	17.2	18.8	17.4	21.4
Width of interorbital space	9.7	12.0	12.3	14.6	14.4	13.8	14.7	10.0	11.4

Two juveniles, 25.0 and 27.5 mm s.l.; R/V *Anton Bruun*, IIOE, Cr. VI; Sta. 353A; 2 July 1964; 1115 to 1925 hrs. l.s.t.; 37°59′S, 64°56′E to 38°15′S, 64°45′E; maximum calculated depth 2394 m; IKMT, deep fraction of catch with Foxton Trousers nominally set at 350 m, specimens probably from below 175 m. MCZ.

One juvenile, 26.5 mm s.l.; R/V *Anton Bruun*, IIOE, Cr. VI; Sta. 354A; 4 July 1964; 0915 to 1510 hrs. l.s.t.; 40°48′S, 65°03′E to 40°51′S, 64°49′E; maximum calculated depth 1650 m; IKMT, considered to be an open net. USNM.

Two juveniles, 24.5 and 25.5 mm s.l.; R/V *Anton Bruun*, IIOE, Cr. VI; Sta. 354B; 4 July 1964; 1605 to 2210 hrs. l.s.t.; 40°51′S, 64°49′E to 40°56′S, 64°25′E; maximum calculated depth 885 m; IKMT, considered to be an open net. SIO.

Description. Morphometric data on the larger specimens are provided in Table 1. Meristic data (value, followed in parentheses by the number of specimens) as follows: first dorsal fin VII (14); second dorsal fin I, 7 (2) or 1, 8 (12); anal fin II, 8 (14); pectoral fin (left side) 18 (9) or 19 (5); gill rakers on first arch 5 (3), 6 (9) or 7 (2) + 1 +13 (1), 14 (1), 15 (5), 16 (5) or 17 (2) totaling 20 to 24; branchiostegal rays 4 + 3 (14); complete scale rows between origin of first dorsal fin and lateral line, 4 (14); between lateral line and origin of anal fin, 14 (1), 15 (11) or 16(2); scales in lateral line from origin to base of mid-caudal ray, 49 (1), 50 (3), 51 (3), 52 (5) or 53 (1); lateral line scales overlying central caudal rays 1 to 4, somewhat correlated with size of fish. Vertebrae, 10 + 14 + 1 = 25 (2).

The notes which follow are based chiefly on the four larger specimens. Observations of juvenile conditions are identified as such. Body compressed and relatively deep; its greatest depth (at origin of dorsal fin) 2.4 to 2.7 in s.l. Greatest width 1.5 to 1.7 in

greatest depth. All of body and head, except for the tip of the snout anterior to the eye and the isthmus, covered by heavy, strongly ctenoid, adherent scales, the cteni of which continue onto the surface of the scale as tranverse ridges. Squamation on the body is complete in our smallest juvenile (24.5 mm s.l.), although the cteni and ridges are poorly developed and the scale coverings on the head and fins are incomplete. The lateral line is well developed. The lateral line scales are produced laterally to form a pair of mid-caudal keels, the beginnings of which are evident in juveniles. Aside from the single simple tranverse tube, the anterior scales of the lateral line are similar to their neighbors. The lateral line continues onto the proximal half of the caudal fin. Other fins are naked.

Distance between snout and origin of first dorsal fin 2.1 to 2.5 in s.l.; preanal distance 1.4 to 1.6 in s.l., preventral distance 2.0 to 2.5 in s.l., prepectoral distance 2.3 to 2.8 in s.l. Spines in fins strong and sharp. Those in first dorsal lie alternately to the right or left of center when the fin is depressed. The second anal and ventral spines are as long or nearly as long as the succeeding soft rays. Pectoral fin set at about 45° with the horizontal, its length 1.4 in length of head. The anus is located about one-fourth of the distance from anal origin to the base of the ventral fin and is separated from the first anal spine by about four scales.

Head broad; interorbital slightly convex, 2.5 to 3.9 in length of head. Eye large, aphakic space small but prominent. Horizontal diameter of eye 2.0 to 2.7 in length of head. Dorsal, and to a lesser extent posterior, edge of orbit spinulose, the spines small and nearly uniform in size. Preopercle with two free edges, the posterior spinulose, the anterior less so or completely without serrations. Opercle, especially its lower half, armed with small simple cteni. Three simple spines, the longest in the middle, present along the upper edge of the opercle.

Gill openings wide. Branchiostegal membranes attached to isthmus but not overlapping. Pseudobranchs present, formed of about 14 filaments. Gill rakers on first arch long and of the usual lath-like shape, those on successive arches reduced to spinulose knobs. Gill filaments notably few and short, those on the first arch no more than half the length of the gill rakers opposite them.

Teeth present on jaws, vomer, and palatines. Tongue toothless. Posterior end of maxillary but little expanded posteriorly and incompletely covered by the suborbitals. Premaxillaries separate and protractile. Each premaxillary bears one to three large antrorse teeth that lie in a horizontal plane and are excluded from the mouth when it is closed. These, as well as the similar teeth at the tip of the lower jaw, are present in juveniles as well as in adults. Premaxillary with a row of minute teeth posterior to the anterior protruding series. Mandibular teeth similar, with antrorse fangs lateral to the median terminal bony boss followed posteriorly by a row of minute teeth. A transverse patch of small teeth present on the vomer, and an irregular band can be found on each palatine.

In alcohol, the adults are uniformly yellowish brown. All fins slightly dusky. Iris and linings of pharyngeal and abdominal cavities black. Juvenile coloration is far more striking. Pigmentation of the caudal part of the body appears last during development; and in young, shorter than 35 mm, the caudal peduncle and fin are completely colorless, while the more anterior part is dark brown or black. There is a darker broad vertical band at about the level of the second dorsal and anal fins, a narrower band through the rear part of the gill cover, and a dark patch on the body ventrally where the black peritoneum can be seen through the body wall. In these young the body coloration is not solid but formed of melanophores more or less closely spaced. When newly caught, the 20–30 mm young showed a ventral reflective zone anterior
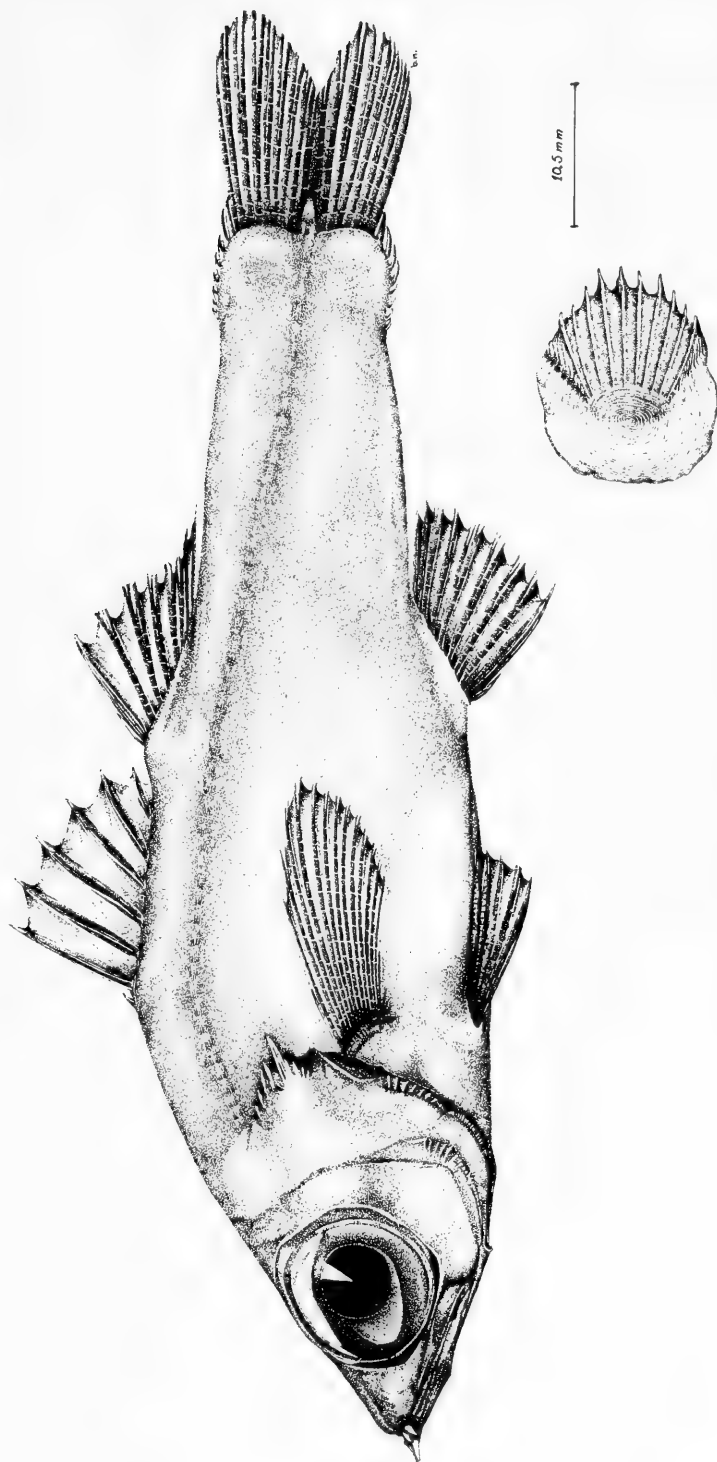
Figure 2. *Florenciella lugubris*, new genus and species; holotype, 89.2 mm in standard length; MCZ 43089. Squamation not shown; the scale illustrated is typical of those on the flank under tip of pectoral fin. Drawn by Basil G. Nafpaktitis.

to the pelvic fins reminiscent of some luminescent systems reported in other cheilodipterid genera (e.g. *Siphamia*, Haneda, 1961), but no structural evidence has been found.

FLORENCIELLA, NEW GENUS

Type species: Florenciella lugubris new species. Gender of generic name: feminine.

Generic characters. This genus most closely resembles *Rosenblattia*, especially by the presence of relatively large antrorse teeth in the anterior parts of both jaws. However, it lacks the mid-lateral caudal keels of *Rosenblattia* and has a less deep body than that genus.

All scales strongly ctenoid. Head almost completely covered by scales; fins largely naked. Lateral line complete, uninterrupted, and extending onto the caudal fin. Mid-lateral scales of caudal peduncle differing from those adjacent to them only by the presence of a lateral line channel. About three rows of scales between base of dorsal fin and lateral line, about seventeen between lateral line and base of anal fin. Strong spines in vertical fins. Two anal spines. Procurrent caudal spines stiff, spiny, and exposed. Eye large, aphakic space prominent. One prominent spine, simple or multifid, at upper end of gill flap which is flanked above and below by lesser spines. Subopercle and preopercle with feeble spines or serrations. Spines present along upper edge of orbit. Teeth present on jaws, palatines, and usually vomer.

FLORENCIELLA LUGUBRIS, NEW SPECIES

Holotype. A 89.2 mm s.l. specimen taken in the equatorial Indian Ocean by R/V *Anton Bruun*, IIOE, Cruise III; Sta. 6, coll. AE13B; 21 August 1963; 0155 to 0440 hrs. l.s.t.; 01°58′S, 60°06′E to 02°06′S, 60°02′E; maximum calculated depth 510 m (depth from t.d.r. 500 m); IKMT, considered an open net collection. MCZ 43089.

Paratypes. Fifty-seven specimens, 22.7 to 97.0 mm s.l.; same data as holotype. Eight specimens in USNM; eight in SIO;

eight in ANSP; three in Zoological Museum, University of Copenhagen; remainder, including one cleared and stained individual, in MCZ.

One, 89.9 mm s.l.; R/V *Anton Bruun*, IIOE, Cr. III; Sta. 5, coll. AE12A; 19 August 1963; 2035 to 2350 hrs. l.s.t.; 01°23′N, 60°11′E to 01°22′N, 60°04′E; maximum calculated depth 750 m (maximum depth from t.d.r. 800 m); shallow fraction of catch with Foxton Trousers set for *ca.* 275 m, specimen probably from above 550 m. MCZ.

Seven, 22.7 to 65.5 mm s.l.; R/V *Anton Bruun*, IIOE, Cr. III; Sta. 6, coll. AE14B; 21 August 1963; 0445 to 1010 hrs. l.s.t.; 02°06′S, 60°02′E to 01°48′S, 59°50′E; maximum calculated depth 1600 m; deep fraction of catch with Foxton Trousers set for *ca.* 275 m, specimens probably taken below 140 m. MCZ and USNM.

Two, 24.7 and 25.9 mm s.l.; R/V *Anton Bruun*, IIOE, Cr. III; Sta. 7, coll. AE15D; 23 August 1963; 0250 to 0610 hrs. l.s.t.; 05°03′S, 60°10′E to 04°52′S, 60°02′E; maximum calculated depth 685 m; deep fraction of catch with Foxton Trousers set for *ca.* 150 m, probably taken below 75 m. MCZ.

One, 26.1 mm s.l.; R/V *Anton Bruun*, IIOE, Cr. III; Sta. 13, coll. AE24A; 8 September 1963; 1055 to 1500 hrs. l.s.t.; 31°58′S, 59°45′E to 32°11′S, 59°30′E; maximum calculated depth 1360 m (depth from t.d.r. 1350 m); deep fraction of catch with Foxton Trousers set for 275 m, probably taken below 110 m. Cleared and stained in MCZ.

One, 26.8 mm s.l.; R/V *Anton Bruun*, IIOE, Cr. VI; Sta. 336B; 27 May 1964; 0047 to 0530 hrs. l.s.t.; 01°50′N, 65°06′E to 01°37′N, 65°07′E; maximum calculated depth 1250 m; deep fraction of catch with Foxton Trousers set for 275 m, probably taken below 140 m. USNM.

One, 26.0 mm s.l.; R/V *Anton Bruun*, IIOE, Cr. VI; Sta. 337A; 27 May 1964; 2130 to 0245 hrs. l.s.t.; 00°03′N, 65°00′E to 00°14′S, 65°03′E; maximum calculated depth 525 m; deep fraction of catch with Foxton

TABLE 2. PROPORTIONAL DIMENSIONS (IN PER CENT OF STANDARD LENGTH) OF A SERIES OF 21 SPECIMENS, INCLUDING THE HOLOTYPE, OF *Florenciella lugubris* CAUGHT BY R/V *Anton Bruun*, IIOE, CRUISE III.

	Sta.13 AE24A	Sta.6 AE13B	Sta.6 AE14B	Sta.6 AE13B				Sta.6 AE14B			Sta.6 AE13B						Holotype AE13B	Sta.5 AE12A	Sta.6 AE13B		
Standard length	26.1	28.8	33.1	36.6	45.6	54.4	57.7	58.9	61.6	65.5	66.2	70.5	73.0	76.0	78.5	84.7	89.2	89.9	90.3	95.4	97.0
Fork length	111.9	108.7	110.3	111.5	109.0	112.7	109.2	111.0	109.1	109.6	108.5	109.2	108.5	110.4	108.9	109.6	108.4	107.4	106.7	107.6	108.2
Greatest depth of body	27.2	26.7	27.8	25.1	26.3	27.6	27.6	28.5	28.4	28.1	25.5	26.9	25.9	27.4	27.4	26.2	29.1	29.6	28.2	28.3	27.5
Least depth of caudal peduncle	10.0	11.1	12.4	11.5	11.4	11.9	13.3	12.7	12.8	11.1	14.1	13.6	13.4	14.1	12.9	13.9	14.3	13.9	13.9	13.8	13.1
Greatest width of body	21.1	14.2	15.4	17.2	17.1	17.1	17.3	17.1	16.2	17.7	16.9	18.4	17.0	17.8	18.1	18.0	17.4	19.7	18.6	18.7	19.2
Snout to origin of first dorsal fin	46.7	44.1	41.4	37.7	41.0	38.8	37.1	38.9	39.9	39.9	39.1	39.0	38.1	38.4	37.5	35.3	38.2	38.3	36.8	38.3	36.8
Snout to origin of anal fin	65.1	62.5	65.0	64.7	63.6	62.5	60.7	61.5	60.5	60.9	60.3	59.4	60.7	60.8	61.5	57.0	59.6	59.3	60.8	58.3	60.4
Snout to insertion of ventral fin	43.7	39.6	37.2	39.6	35.7	37.3	37.3	37.7	36.2	37.3	36.1	35.0	36.3	37.4	35.8	36.4	33.7	34.6	35.2	34.6	35.4
Snout to insertion of pectoral fin	40.6	36.8	35.9	35.8	33.8	34.7	33.4	33.8	33.8	34.8	33.2	32.8	32.6	34.2	32.6	33.2	31.9	33.5	33.8	31.1	33.0
Length of base of first dorsal fin	16.1	13.9	13.9	14.2	13.6	12.5	13.7	13.4	16.2	15.1	12.5	13.6	15.8	15.7	12.7	13.3	13.7	13.7	13.5	14.5	14.3
Length of base of second dorsal fin	10.3	11.1	11.2	10.9	10.5	10.7	11.4	11.5	9.7	11.5	10.3	11.1	10.7	11.1	10.6	10.4	11.5	11.0	10.4	10.9	11.1
Distance between first and second dorsal fins	8.0	6.9	9.1	8.7	7.5	9.6	9.7	9.8	4.7	8.6	9.1	9.5	9.7	8.9	10.3	8.6	8.4	11.0	9.3	9.0	10.3
Length of base of anal fin	13.8	10.7	10.6	11.2	9.4	11.0	11.3	11.4	11.0	11.1	10.6	9.4	10.8	11.2	10.7	11.3	11.2	11.1	10.4	10.7	11.0
Distance between anus and insertion of ventral fin	17.6	19.4	18.1	18.9	19.5	18.9	18.2	17.1	18.8	17.7	19.9	20.8	19.9	19.0	19.5	18.1	20.2	19.7	18.8	19.8	16.4
Distance between anus and origin of anal fin	6.1	5.2	8.2	8.2	7.5	5.5	7.8	7.0	6.3	5.8	7.1	6.1	6.4	6.6	7.3	6.0	6.8	7.3	6.8	6.0	6.8
Length of pectoral fin	23.8	21.5	26.0	24.6	20.8	24.4	24.4	24.6	23.2	25.0	24.8	23.0	22.2	23.6	22.9	23.0	22.6	22.2	21.6	20.4	21.2
Length of ventral fin	19.9	16.7	17.8	18.3	16.7	17.6	16.5	17.1	17.9	15.1+	14.5	15.9	15.5	16.2	15.3	15.0	15.1	12.3+	15.5	14.7	14.9
Length of head	40.6	37.5	35.0	32.5	35.7	36.0	34.7	34.0	34.2	35.1	32.5	33.2	32.1	33.8	32.5	31.9	34.1	33.5	32.4	34.2	33.5
Length of snout	10.7	9.7	9.4	7.4	7.0	9.2	6.4	7.5	6.8	8.6	6.3	6.9	7.0	7.8	7.1	6.8	7.0	7.3	7.2	6.4	7.2
Length of upper jaw	19.5	19.1	18.2	18.0	16.9	16.5	16.1	16.8	16.4	16.3	15.9	15.9	15.6	15.8	14.9	14.4	15.0	13.6	14.6	15.0	15.2
Horizontal diameter of eye	19.5	16.7	16.0	15.8	15.4	14.3	15.6	15.8	15.1	15.3	13.8	13.8	14.5	14.2	13.2	13.4	13.5	13.6	12.7	12.8	13.6
Width of interorbital space	13.4	8.3	9.4	9.0	9.9	10.7	9.5	10.0	9.4	9.5	10.1	10.1	9.2	11.1	10.4	9.8	10.3	9.9	10.4	9.5	9.7
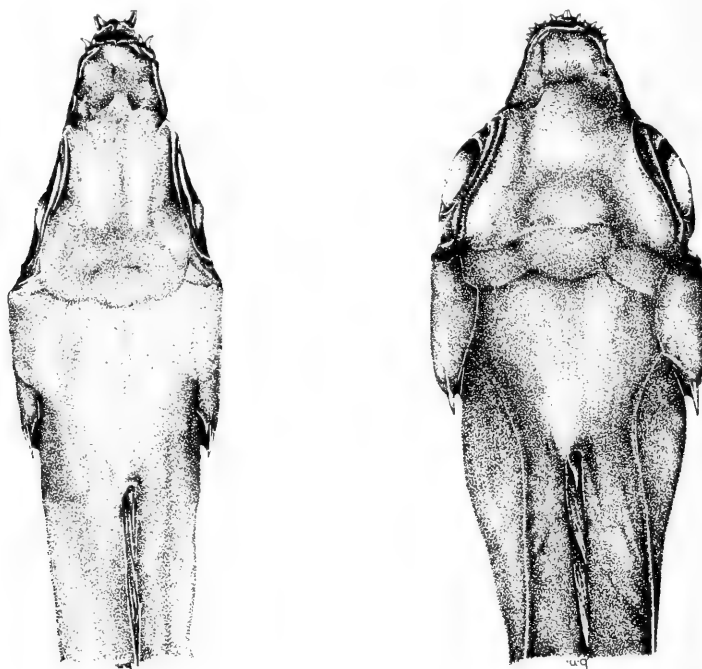
Figure 3.   Dorsal views of heads of *Rosenblattia robusta* (left) and *Florenciella lugubris* (right).   Squamation not shown. Drawn by Basil G. Nafpaktitis.

Trousers set for 275 m, probably taken below 140 m. MCZ.

Description. Morphometric data, taken from the type and a series of paratypes, are provided in Table 2. Meristic data were taken from fifty specimens including the type. These data (value, followed in parentheses by the number of specimens) follow: first dorsal fin VII (50); second dorsal fin I, 8 (50); anal fin II, 8 (49) or rarely II, 7 (1); pectoral fin (left side, or if damaged the right) 16 (1), 17 (28), 18 (20) or 19 (1); gill rakers on first arch 5 (1), 6 (39) or 7 (10) + 1 + 14 (16), 15 (32) or 16 (2) totaling 20 (2), 21 (13), 22 (24) or 23 (11); branchiostegal rays 4 + 3 (50); complete rows of scales between origin of first dorsal fin and lateral line 4 (50); between lateral line and origin of anal fin 15 (5), 16 (37) or 17 (8); scales in lateral line from origin to base of mid-caudal ray 49 (3), 50 (14), 51 (18), 52 (8) or 53 (7);

one to four lateral line scales on caudal fin, some of these frequently missing and apparently more numerous in larger than in smaller specimens. Vertebrae, 10 + 14 + 1 = 25 (8) or 10 + 13 + 1 = 24 (1).

Body compressed and relatively shallow, its greatest depth (at origin of first dorsal fin) 3.3 to 3.8 in s.l., its greatest width (immediately behind orbit) 1.3 to 1.8 in greatest depth. All of body and head, except for the snout anterior to eye, covered by adherent ctenoid scales, the cteni of which are continuous with transverse ridges on the surface of each scale. Squamation essentially complete at 30 mm s.l., but at this size the cteni and associated ridges are scarcely evident. Scales of lateral line normal, the line terminating with one, two or three pored scales overlying central rays of the caudal fin. The other fins, both paired and vertical, are naked and there are no axillary scales.

Distance between snout and origin of first dorsal fin 2.2 to 2.8 in s.l.; preanal distance 1.5 to 1.8 in s.l.; preventral 2.3 to 2.9 in s.l.; prepectoral 2.5 to 3.2 in s.l. Spines in fins strong, high and sharp, those in the first dorsal fin lying alternately on the right or left of center when the fin is depressed. Dorsal and second anal spines about as long as the soft rays which follow them; spiny elements in the vertical fins longer than the soft. Base of pectoral fin set at about 45° angle with the horizontal, the fin relatively short and rounded, its length 1.4 to 1.7 in length of head. Anus located about one-fourth of the way from origin of anal to insertion of ventral fins and separated from the first anal spine by about five scales. Head broad and bony, its greatest width 1.7 to 2.3 in length of head, its length 2.5 to 3.1 in s.l. Interorbital nearly flat, its least bony width 3.0 to 3.7 in length of head. Eye large, its horizontal diameter 2.1 to 3.0 in length of head. Pupil elliptical, aphakic space prominent. Dorsal and posterior edges of orbit spinulose, the supraorbital ridge terminating anteriorly in a broad, flat spine. Free edge of preopercle single, usually smooth, but occasionally (especially in smaller individuals) bearing a few minute spines. A complex cluster of spines originate near the more posterior part of the opercular bone. The largest spine is the most posterior; it is usually simple in smaller specimens, but compound in the larger. Smaller and more or less simple spines lie above and below that at the angle of the operculum. Elsewhere the free edge of the gill cover is either smooth or weakly serrated.

Gill openings wide, the gill flaps and branchiostegal membranes meeting at the ventral midline but not overlapping. Pseudobranchs present, formed of about 14 filaments. Gill rakers on first arch of the usual lath-like shape and about half as long as diameter of eye. Gill filaments unusually short and few, those of first arch about two-thirds as long as the opposite rakers.

Symphysis of upper jaw toothless. On each side lateral to the midpoint is a patch of minute teeth and two or three conical, slightly recurved antrorse teeth. A single series of minute teeth is present on the more posterior biting edge of the premaxilla. The two or three conical antrorse canines on the mandible are followed by a row of small teeth. The vomer may bear a few minute, sharp teeth or be completely toothless. Palatines with teeth in a simple series or in a band. Tongue toothless.

In alcohol, the flanks are uniformly dusky, with more pigment along the margins of the scale pockets than elsewhere and with darker areas along the bases of the vertical fins. All fins are dark brown. The eye is dark, but elsewhere the head is similar in pigmentation to the body. Linings of mouth, pharynx, and abdominal cavity black. In young of about 35 mm s.l., the black linings of the body cavities are evident through the lighter dermal pigmentation, the black bases of the second dorsal and anal fins contrast in a more striking way with the pale flanks, the tip of the caudal is black, and there is a prominent dark vertical bar across the caudal peduncle in an area bounded by the upper and lower procurrent caudal rays.

HOWELLA BRODIEI OGILBY 1898

The three nominal species of *Howella* have never been critically compared. The type specimen of *Howella brodiei* was found on the beach at Lord Howe Island near Australia. The type locality for the second species, *H. sherborni* (Norman, 1930, as *Rhectogramma sherborni*) lies in the eastern Atlantic off South Africa, *ca.* 34°S, 17°E. The third species, *H. pammelas* (Heller and Snodgrass, 1903, as *Galeagra pammelas*) was first taken at Wenman Island in the Galapagos group.

The type of *H. pammelas* (Heller and Snodgrass, 1903: pl. 4) and additional eastern Pacific material of this species from the collections of Scripps Institution of Oceanography show both an upper and a lower opercular spine to be complex. In

contrast, only the upper opercular spine is complex in specimens of *Howella* from the western Pacific and Atlantic. On this basis alone, other morphometric data being similar, our Indian Ocean specimens, all of which have only an upper complex opercular spine, are referred here to *H. brodiei*, a species of which *H. sherborni* is tentatively considered conspecific. A critical and more detailed examination of the now considerable material from all oceans is obviously in order.

This genus is hitherto unknown from the Indian Ocean, the nearest records being the South African-Atlantic type locality of *H. sherborni*, the Australian type locality of *H. brodiei*, and a Philippine locality reported for the latter species by Herre and Herald (1951).

The *Anton Bruun* took specimens of *H. brodiei* at each of the following twelve stations:

One, 18.0 mm s.l.; Cr. III; Sta. 2, coll. AE6E; 15 August 1963; 0350 to 0715 hrs. l.s.t.; 10°09′N, 59°55′E to 10°00′N, 60°01′E; maximum calculated depth 560 m (depth from t.d.r. 520 m); IKMT, deep fraction of catch with Foxton Trousers nominally set for 150 m, specimen probably taken below 75 m. MCZ.

One, 14.5 mm s.l.; Cr. III; Sta. 3, coll. AE8B; 16 August 1963; 1845 to 2213 hrs. l.s.t.; 06°54′N, 59°55′E to 06°37′N, 59°57′E; maximum calculated depth 750 m; IKMT, shallow fraction of catch with Foxton Trousers set for 150 m, probably taken above 300 m. MCZ.

One, 13.6 mm s.l.; Cr. III; Sta. 5, coll. AE12B; 19 August 1963; 2035 to 2350 hrs. l.s.t.; 01°23′N, 60°11′E to 01°22′N, 60°04′E; maximum calculated depth 750 m (depth from t.d.r. 800 m); IKMT, shallow fraction of catch with Foxton Trousers set for 275 m, probably taken above 550 m. Zoological Museum, University of Copenhagen.

One, 65.0 mm s.l.; Cr. III; Sta. 7, coll. AE16D; 23 August 1963; 0625 to 1350 hrs. l.s.t.; 04°52′S, 60°02′E to 04°27′S, 59°55′E; maximum calculated depth 2030 m; IKMT,

deep fraction of catch with Foxton Trousers set at 275 m, probably caught below 140 m. MCZ.

One, 42.5 mm s.l.; Cr. III; Sta. 16, coll. AE30B; 12 September 1963; 1110 to 1710 hrs. l.s.t.; 40°53′S, 60°01′E to 41°07′S, 59°52′E; maximum calculated depth 2750 m; IKMT, deep fraction of catch with Foxton Trousers set for 275 m, probably taken below 140 m. SIO.

One, 61.0 mm s.l.; Cr. III; Sta. 16, coll. AE31B; 12 September 1963; 1725 to 2105 hrs. l.s.t.; 41°07′S, 59°52′E to 41°07′S, 60°08′E; maximum calculated depth 635 m; IKMT, deep fraction of catch with Foxton Trousers set for 150 m, probably from below 75 m. MCZ.

Two, each 14.6 mm s.l.; Cr. VI; Sta. 334A; 24 May 1964; 1912 to 2345 hrs. l.s.t.; 06°01′N, 64°59′E to 05°48′N, 64°57′E; maximum calculated depth 700 m; IKMT, deep fraction of catch with Foxton Trousers set for 275 m, probably taken below 140 m. MCZ.

One, 47.0 mm s.l.; Cr. VI; Sta. 335 B; 26 May 1964; 0100 to 0850 hrs. l.s.t.; 03°46′N, 65°05′E to 03°27′N, 65°07′E; maximum calculated depth 2575 m; IKMT, deep fraction of catch with Foxton Trousers set for 275 m, probably taken below 140 m. USNM.

One, 15.5 mm s.l.; Cr. VI; Sta. 337B; 28 May 1964; 0300 to 0930 hrs. l.s.t.; 00°14′S, 65°03′E to 00°29′S, 65°08′E; maximum calculated depth 2250 m; IKMT, shallow fraction of catch with Foxton Trousers set for 275 m, probably taken above 550 m. USNM.

Three, 11.8 to 14.6 mm s.l.; Cr. VI; Sta. 340B; 31 May 1964; 1945 to 0155 hrs. l.s.t.; 05°55′S, 64°48′E to 06°08′S, 64°58′E; maximum calculated depth 746 m; IKMT, shallow fraction of catch with Foxton Trousers set for 275 m, probably taken above 550 m. MCZ.

Two, 11.1 and 11.9 mm s.l.; Cr. VI; Sta. 341B; 1–2 June 1964; 2200 to 0300 hrs. l.s.t.; 07°56′S, 65°14′E to 07°57′S, 64°51′E; max-

imum calculated depth 504 m; IKMT, considered an open net. MCZ.

Three, 10.2 to 12.4 mm s.l.; Cr. VI; Sta. 342A; 2 June 1964; 1755 to 2250 hrs. l.s.t.; 09°57'S, 64°55'E to 10°01'S, 64°19'E; maximum calculated depth 580 m; IKMT, deep fraction of catch with Foxton Trousers set for 200–250 m, probably taken below 125 m. MCZ.

BATHYSPHYRAENOPS PARR 1933

Bathysphyraenops, a monotypic genus, has been known only from the type series of *B. simplex* Parr 1933, which was taken off the Bahamas and adjacent islands, and from unpublished catches made elsewhere in the Atlantic and Pacific. Our Indian Ocean collection contains two specimens, 84.5 and 90.8 mm s.l., which we have critically compared with the holotype of *B. simplex* (Bingham Oceanographic Lab. no. 2847). Meristic values, with the possible exception of the number of scale rows between the lateral line and origin of anal fin, are nearly identical, and differences in body proportions, armature, etc. are insignificant. These Indian Ocean *B. simplex* were taken at the following station:

R/V *Anton Bruun*, IIOE, Cr. III; Sta. 6, coll. AE13B; 21 August 1963; 0155 to 0440 hrs. l.s.t.; 01°58'S, 60°06'E to 02°06'S, 60°02'E; maximum calculated depth 510 m (depth from t.d.r. 500 m); IKMT, considered an open net. MCZ and USNM.

BRINKMANNELLA PARR 1933

Included within the small group of oceanic cheilodipterids with single anal spines and unarmed opercular flaps are *Brinkmannella elongata* Parr, previously known only from midwaters off the Bahama Islands (Parr, 1933:26), and *Brephostoma carpenteri* Alcock, an abyssal benthic species from the Bay of Bengal (Alcock, 1889:383). *Brinkmannella elongata* has deciduous scales and teeth in jaws, palatines, and vomer. *Brephostoma carpenteri* has adherent scales and a toothless mouth. In other respects the two genera are suspiciously similar.

Our Indian Ocean material contains two lots of specimens within this group. The first is a single individual, 104.5 mm s.l., which is larger but otherwise identical to the Atlantic *Brinkmannella elongata*. It was taken as follows:

Scripps Institution of Oceanography "Monsoon" Expedition; IKMT haul no. 9; 19 December 1960; 0324 to 0829 hrs. l.s.t.; 33°19'18"S, 72°34'24"E to 33°38'06"S, 72°31'00"E; maximum calculated depth 1878 m, open net. SIO 61–37.

The second lot contains four fishes, *ca.* 64-*ca.* 103 mm s.l., all in poor condition, which are meristically more similar to *Brephostoma carpenteri* than to *Brinkmannella elongata* but show the generic characters diagnostic of this latter genus: teeth in jaw, palatines, and vomer; deciduous scales; and an area of relatively light pigmentation on the flanks posterior to the anal fin. These are characters which possibly could change as a pelagic young assumes a benthic adult life. Therefore, pending further study, the identity of this lot is left open as "*Brinkmannella* sp." The series came from the following locality:

R/V *Anton Bruun*, IIOE, Cr. III; Sta. 6, coll. AE13B; 21 August 1963; 0155 to 0440 hrs. l.s.t.; 01°58'S, 60°06'E to 02°06'S, 60°02'E; maximum calculated depth 510 m (depth from t.d.r. 510 m); IKMT, considered an open net. MCZ.

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Italian Wolf Spiders of the Genus *Pardosa* (Araneae: Lycosidae)

by **PAOLO TONGIORGI**

Museum of Comparative Zoology, Cambridge, Massachusetts
Istituto di Biologia Generale, Università di Pisa, Italy

ITALIAN WOLF SPIDERS OF THE GENUS *PARDOSA* (ARANEAE: LYCOSIDAE)

PAOLO TONGIORGI

We owe to Giovanni Canestrini and Pietro Pavesi the first accurate work on Italian spiders. Their memoir was presented at the Congresso dei Naturalisti Italiani in Vicenza in 1868, and was published in Atti della Società italiana di Scienze naturali in Milan under the title "Araneidi Italiani." This work records 404 species, 38 of which belong to the family Lycosidae. Among these are only 12 species of *Pardosa*, just one-third of the *Pardosa* species known at present for the Italian spider fauna. During the ensuing years, the largest harvest of information on the Italian spider fauna has been gathered by L. Di Caporiacco (1922–1953) and some recent foreign authors who have made further contributions. These authors have very often limited themselves to compilation of faunal lists concerning more or less limited areas of the peninsula. There are hardly any works on single taxonomic groups. My attempt to satisfy the need for work on the spiders of the genus *Pardosa* has not been easy and is still far from furnishing a true picture of Italian species. In particular, the data on the geographical distribution of different species are scanty and doubtful. Often we have little or no information about the species of certain regions that are of interest because of their geographical position and past geological events—Sicily for example. One of the greatest difficulties in attempting to reconstruct a reliable picture of Italian distribution of *Pardosa* results from the inability to

check the numerous records. Most of the collections are lost or their present locations are unknown. Other collections, such as the spiders of Carnia collected and identified by Di Caporiacco (1922, 1927), revealed a very high number of errors or identifications based on juvenile specimens. The same specific name was sometimes used for different species so it is impossible to know which species the older authors intended. Among the Italian species of the genus *Pardosa* I have included those found near the political boundaries of Italy, where there are no ecological or geographical reasons that would exclude them. That these species are not found in Italy probably can be ascribed to lack of collecting rather than to their real absence.

As a general rule the descriptions and drawings were made from specimens collected in Italy. When that was impossible, I used specimens from the localities nearest to Italy; in all cases I have indicated where the specimens were collected. In this way I was able to examine and make original drawings of specimens of all the species. The present study used mainly specimens I collected myself and material coming from the collections of Museo Civico di Storia Naturale, Genova (MSNG), Museum of Comparative Zoology, Cambridge (MCZ), and Museo di Storia Naturale, Firenze (MSNF). Other specimens were borrowed from the following collections: Istituto di Zoologia dell'Università, Padova (Collection

Canestrini) (IZUP); Muséum d'Histoire Naturelle, Genève (MHNG); Muséum National d'Histoire Naturelle, Paris (MNHN); Museo di Storia Naturale, Verona (MSNV); Naturhistoriska Riksmuseum, Stockholm (RMS); Senckenberg Museum, Frankfurt (SMF); and Professor P. Zangheri's Romagna arachnids (Forlì) (CZ). When necessary the types of the species were examined.

Routinely, the drawings of the left male palpus illustrate the ventral and ventrolateral views. In the ventrolateral view the palpus is rotated about 60°, a position that shows the terminal apophysis equally well in all species. The terms tegular and terminal apophysis are used according to Holm (1947). While the tegular apophysis is homologous in all species, the terminal apophysis does not originate always from the same piece (Fig. 1). The different parts of the epigynum are illustrated on Figure 2. Only the external view of the female genitalia was drawn. Since the body pattern may be a helpful and distinctive character for the females, this was illustrated for some species. For each group of species that has a similar body pattern it was illustrated only once. The descriptions of the patterns are mainly based on female specimens as the patterns of the males are similar but often darker and less distinct; when the male differs in some character, it is pointed out. When possible, specimens were selected to represent the mean of the specific variability. When considerable variability occurred I provided more than one drawing. All drawings were made with the specimens submerged in 80 per cent alcohol under a dissecting microscope provided with a reticule grid in the ocular.

Generally, the Italian species of the genus *Pardosa* are not difficult to identify, except those of the *P. monticola* group. More information about this group and its relationships with the species not belonging to the Italian fauna will be published in a separate paper (Tongiorgi, 1965). For each species I listed the original reference. Only when I changed the synonymy were other references listed. For additional sources consult the bibliographic works of Bonnet (1958), and Roewer (1954). In the descriptions of species only characters useful for identification are discussed. I could not check most of the records because, as I mentioned above, the animals were often not preserved, or were lost, or for the greater part of Di Caporiacco's collections, labels in the vials were not clear. Concerning the Italian distribution of each species, I have deliberately omitted all data that I have been unable to check personally. The distribution that could be constructed from this group of data must be considered only a tentative one. In fact, many records, in particular those of Di Caporiacco, are scarcely reliable. For example, among the *Pardosa* from Romagna of Zangheri's collection, determined by Di Caporiacco, only the specimens of three vials were correctly identified. Thus the list of localities gives only those from which

I could examine specimens, the name of the collectors, and where the specimens are now deposited. If there are no such indications, the specimens are collected by me and kept in my own collection. I have indicated for each species where the type is preserved. The geographical distributions outside Italy are taken from the compilations of Bonnet (1958) and Roewer (1954) and may not be accurate.

Key to Italian species of genus PARDOSA

1. Males 2
 – Females 41
2. Tegular apophysis as in Figures 100–118, terminal apophysis variable. (The species belonging to *P. monticola* group constitute a homogeneous group) (*P. monticola* group) 3
 – Tegular apophysis different 12
3. Tarsi, metatarsi and part of tibiae of first pair of legs covered with long hairs (Fig. 106), much longer than on the corresponding segment of other legs. Terminal apophysis beak-like (Figs. 104–105) ....
 .... *P. mixta*
 – Tarsi, metatarsi and tibiae of first pair of legs with hairs as long as those on other legs 4
4. Terminal apophysis large, well developed, more or less pointed, and jagged at the apical end (Figs. 102, 103) .... *P. palustris*
 – Terminal apophysis small and different 5
5. Terminal apophysis with two small blunt teeth (Figs. 107, 108), median light band of carapace dilated in front .... *P. agricola*
 – Terminal apophysis with one tooth only or without teeth 6
6. Median light band of carapace dilated in front, lateral band broken 7
 – Median light band dilated or pointed, lateral bands continuous 8
7. Terminal apophysis pointed, with a stout tooth (Figs. 109, 110) .... *P. torrentum*
 – Terminal apophysis without tooth (Figs. 100–101) .... *P. agrestis* (part.)
8. Median light band of carapace dilated anteriorly (Fig. 95), terminal apophysis without tooth .... *P. agrestis* (part.)
 – Median light band pointed anteriorly (Fig. 96) 9
9. Terminal apophysis without tooth ....
 .... *P. agrestis* (part.)

 – Terminal apophysis stout, more or less tooth-shaped 10
10. Segments of male palpus without white hairs, terminal apophysis small and slender, tegular apophysis generally long and rather pointed (Figs. 111, 112) .. *P. monticola*
 – Segments of male palpus more or less covered with white hairs 11
11. Femur, patella, tibia and part of tarsus with white hairs; palpus as in Figures 117, 118 .... *P. albata*
 – Femur and patella only with white hairs; palpus as in Figures 115, 116 .... *P. blanda*
12. Anterior tibia with four pairs of spines on ventral sides as well as a pair of little apical ones. Palpus as in Figures 123, 124. (The species of genus *Acantholycosa* generally have five or more pairs of spines on ventral sides of first tibia and genitalia very different.) .... *P. nigra*
 – Anterior tibia with two pairs of spines as well as apical pair (in some cases the anterior lateral pair of spines almost fall into line with the ventral pairs and it may appear that there are three pairs of ventral spines) 13
13. Tegular part of bulb very protuberant. From the shield protrudes a slender and pointed process bent towards the external side 14
 – Tegular part of bulb otherwise 15
14. Embolus long and distally pointed (Figs. 15, 16, 17) .... *P. giebeli*
 – Embolus flattened, making an angle at level of process of shield, then ending with a flattened and expanded lamina, anteriorly pointed and forwardly directed (Figs. 19, 20, 22) .... *P. eiseni luciae*
15. Some spinnerets black 16
 – Spinnerets yellow or brown, sometimes very dark but never black 19
16. All spinnerets black. Palpus as in Figures 67, 68 .... *P. saltuaria*
 – Anterior spinnerets black, other spinnerets more or less dark 17
17. Tegular apophysis a robust lamina, C-shaped. Terminal apophysis a big tooth (Figs. 30, 31). Lateral bands of carapace narrow. Abdomen with reddish pattern
 .... *P. lapponica*
 – Tegular apophysis differently formed. Terminal apophysis otherwise. Lateral bands of carapace rather wide. Abdomen with very clear yellow pattern (Figs. 3,

11) 18

18. Looking at the palpus in ventral position, the tegular apophysis seems a more or less circular lamina with a sharp tooth on the middle. The tooth is more evident as seen from the side (Figs. 12, 13) ....*P. schenkeli*

— In ventral position, the tegular apophysis has a hooked laminal process on the external side (Figs. 8, 9) .... *P. bifasciata*

19. Metatarsi of the second pair of legs ventrally with long hairs, much longer than on other legs (Fig. 6). Palpus as in Figures 4, 5 .... *P. vittata*

— Metatarsi of the second pair covered with hairs of the same length as on other pairs   20

20. Tegular apophysis long, extending beyond the edge of alveolus or close to it. The upper branch of the apophysis is directed anteriorly and laterally, sometimes pointed, sometimes apically blunted   21

— Tegular apophysis short, variously formed. If the apophysis has an upper branch, it is far from the alveolar edge   29

21. Terminal apophysis long and narrow, finger-shaped (Figs. 39, 40) .... *P. nigriceps*

— Terminal apophysis absent (or at least not visible) or a thin lamina (*P. lugubris*)   22

22. Tegular apophysis robust and apically blunted and does not reach the edge of alveolus. The shield has a robust and laterally directed process   23

— Tegular apophysis pointed or blunted but always close to the edge of the alveolus as observed from the ventral side   24

23. Palpus as in Figures 36, 37 .... *P. ferruginea*

— Palpus as in Figures 34, 35 .... *P. cavannae*

24. Median light band of carapace wide, covered with white hairs, lateral bands not very distinct. Tarsal article of palpus narrow and long, covered with short hairs. Terminal apophysis a thin lamina (Figs. 56, 57) .... *P. lugubris*

— Median light band of carapace more or less distinct, generally more evident on the thoracic region, spindle-shaped or more or less branched. Tarsal article of palpus not as narrow as in *P. lugubris*   25

25. Median light band slightly branched on the thoracic region; lateral bands clearly broken or absent. Tibial and tarsal segments of palpus black, thickly covered with black hairs. Palpus as in Figures 60, 61 .... *P. amentata*

— Median light band of carapace as in Figure 44, generally reddish and not distinct; lateral bands continuous or a little broken with two or three lines. Segments of palpus reddish. Tegular apophysis, as seen from the ventral side, seems to have two independent pieces. The one directed anteriorly and laterally is more or less pointed distally; the other is directed laterally and has the point bent as a hook (Figs. 42, 43) (*P. riparia* group)   26

26. Tegular apophysis very long and distally blunt, extending beyond the edge of alveolus (Figs. 42, 43) .... *P. riparia*

— Tegular apophysis long, more or less pointed, reaching scarcely to the edge of alveolus or extending beyond it only a little   27

27. Tegular apophysis pointed, scarcely reaching the edge of alveolus if the palpus is observed from the ventral side. If the palpus is observed from the lateral side the point of tegular apophysis is far from the edge of alveolus (Figs. 49, 50) .... *P. pullata*

— Tegular apophysis apically blunt, reaching to the edge of alveolus (observed either ventrally or laterally)   28

28. The distal point of tegular apophysis extends beyond the edge of alveolus. Ectal corner of tegulum pointed and strongly sclerotized (Figs. 46, 47) .... *P. femoralis*

— The distal point of apophysis scarcely reaches edge of alveolus. Ectal corner of tegulum slightly pointed, visible and not sclerotized (Figs. 53, 54) .... *P. prativaga*

29. Tegular apophysis with upper branch always clear, more or less bent as a hook. Point of the lower branch of apophysis directed toward the median side of the palpus. (Left side if the left palpus has been observed from ventral side)   30

— Tegular apophysis squat. There is not an upper branch, or if present it is not bent laterally. Sometimes the apophysis has a laminar shape (*P. nebulosa*)   35

30. Upper branch of tegular apophysis ending with a sharp point. Lateral bands of carapace continuous or hardly broken with two or three lines, sometimes absent   31

— Upper branch of the tegular apophysis distally blunt. Lateral bands clearly broken or continuous but not very clear   32

31. Palpus as in Figures 26, 27. Upper branch of tegular apophysis short. The shield, as

seen from the side, has an anteriorly bent lamina as in Figure 27 _____ *P. sordidata*
– Palpus as in Figures 23, 24. Upper branch of tegular apophysis long. The shield is differently formed _____ *P. paludicola*
32. Segments of palpus dark brown _____ 33
– Segments otherwise, distal part of femora, patella and tibia of the palpus yellow on upper side, black ventrally. Lateral bands continuous. Palpus as in Figures 139, 140. This species lives only on salt marshes ____ _____ *P. luctinosa*
33. Tegular apophysis strongly C-shaped _____ 34
– Tegular apophysis as in Figures 135, 136. Lateral bands clearly broken _____ *P. italica*
34. Found in plains to 1400 m along the edges of rivers and streams with preference for pebbly banks. Body pubescence gray. Length of tarsal segment of palpus 1 mm. Total length of body 5 to 6 mm. Palpus as in Figures 128, 129 _____ *P. wagleri*
– Found on high mountains, along the edges of streams, on moraines, and often under stones that cover the glaciers. Bigger than the preceding species. Body color generally dark, almost black. Length of tarsal segment of palpus 1.5 mm. Length of body 7–8 mm. Palpus as in Figures 132, 133 _____ *P. saturatior*
35. Tegular apophysis as a lamina slightly slanted towards the external side. Palpus as in Figures 119, 120. Species large. Total body length 8.25 mm (only 1 male examined) _____ *P. nebulosa*
– Tegular apophysis different. It generally has a tooth, the point of which is sometimes bent towards the lateral side, sometimes towards the median one _____ 36
36. Shield with a laminar process _____ 37
– Shield without laminar process _____ 40
37. Laminar process of the palpal shield, as seen from ventral side, appears strongly lengthened and pointed _____ 38
– Laminar process of the shield short _____ 39
38. Tegular apophysis thumb-shaped (Figs. 158, 159) _____ *P. strigillata*
– Tegular apophysis as in Figures 160, 161 _____ *P. pseudostrigillata*
39. Tooth of tegular apophysis directed towards the ectal side (Figs. 154, 155), very common _____ *P. hortensis*
– Tooth of tegular apophysis directed towards the mesal side of the palpus (Figs. 64, 65) _____ *P. morosa*

40. Lateral bands of carapace continuous, though not very distinct. Tegular apophysis broader than long. Terminal apophysis as in Figures 152, 153 _____ *P. cribrata*
– Lateral bands of carapace broken. Tegular apophysis longer than broad. Terminal apophysis as in Figures 156, 157, very common _____ *P. proxima*
41. Septum of epigynum shaped as a trapezoidal plate of reddish color covering the genital depression. (*Pardosa monticola* group and *P. saltuaria*) _____ 42
– Septum of epigynum rather reduced and different. If it occupies the genital depression it is triangular _____ 52
42. Anterior spinnerets dark brown or black. Septum with edges of the posterior half strongly rounded (Fig. 69) _____ *P. saltuaria*
– Spinnerets yellow _____ 43
43. Median light band of carapace tapering, pointed in front or ending with a small diamond-shaped spot _____ 44
– Median band clearly dilated behind the posterior eyes and at level of thoracic furrow _____ 49
44. Lateral bands of carapace broken by two or three lines (Fig. 90). Edge of the anterior pockets as in Figures 88, 89 _____ _____ *P. blanda* (part.)
– Lateral bands of carapace continuous _____ 45
45. Genital septum longer than broad. Edge of the septum almost parallel or slightly enlarged posteriorly. Edge of the anterior pockets as in Figure 83. Legs light, more or less annulated _____ *P. monticola*
– Genital septum broader than long _____ 46
46. Septum clearly much broader than long. Edge of the anterior pockets regularly curved as in Figures 84, 85, 88, 89 _____ 47
– Septum becoming large posteriorly with more or less sinuous sides. Edges of the anterior pockets never regularly curved as in *P. blanda* and *P. palustris* _____ 48
47. Posterior angles of septum obtuse, often wrinkled and prominent. Septum with a longitudinal deep groove, about two-thirds its length (Figs. 84, 85). Legs generally light ___ _____ _____ _____ _____ *P. palustris*
– Posterior lateral extensions of the septum sometimes extending laterally, sometimes pointed anteriorly, never wrinkled (Figs. 88, 89). Legs, especially femora, dark _____ *P. blanda* (?*P. albata*)

48. Sides of septum almost parallel, with posterior angles more or less blunted and often a little wrinkled. Carapace pattern as in *P. blanda*, but the lateral bands are always continuous, and near the edges of the carapace there is another thin light band (Figs. 80, 81, 93) .... *P. mixta*
— Sides of the septum rather sinuous, with the posterior angles generally beak-shaped. Legs more or less annulated (Figs. 72–74) .... *P. agrestis* (part.)
49. Lateral light bands of carapace broken 50
— Lateral bands continuous (Fig. 95). Epigynum as in Figures 72–74 ...... *P. agrestis*
50. Septum about as broad as long, sides S-shaped. Edges of the anterior pockets as in Figures 77–79. Legs clearly annulated .... *P. agricola*
— Septum broader than long. Legs annulated or not 51
51. Legs annulated. Edge of the anterior pockets as in Figures 86, 87. Abdominal pattern yellow reddish, rather pronounced (Fig. 99) .... *P. torrentum*
— Legs scarcely annulated. Sides of septum regularly enlarged, only a little sinuous. Edge of the anterior pockets as in Figures 72–74 .... *P. agrestis* (part.)
52. Anterior tibia with four pairs of spines on ventral side. Epigynum as in Figure 125. Body color very dark .... *P. nigra*
— Anterior tibia with two pairs of spines on ventral side (occasionally three pairs) .. 53
53. Lateral bands of carapace continuous, broad, often as broad as the dark bands. They are marginal. A dark band more or less distinct is included on the light ones. Median light band broad. On the abdomen, as well as on the anterior lanceolate stripe, a yellow pattern is very distinct (compare Figs. 3, 11). Carapace rather long and narrow 54
— Lateral bands continuous or broken, always narrower than the dark ones and divided from the edges of carapace by a narrow dark band. Carapace not particularly lengthened (except *P. nigriceps*) 56
54. Spinnerets yellow. Anterior portion of of the genital depression long and narrow. The two lips rather undulating. Posterior portion trapezoidal in shape. Epigynum as in Figure 7 .... *P. vittata*

— Anterior spinnerets black or at least darker, especially at the base. Epigynum very small, yellowish. The seminal receptacles can be seen through the cuticle 55
55. Only one anterior pocket with rounded edge under which median septum of epigynum is tucked. The connecting canals of the seminal receptacles coil once (Fig. 10) .... *P. bifasciata*
— Two anterior pockets. Median septum long and undulating. The connecting canals of the seminal receptacles coil at least twice (Fig. 14) .... *P. schenkeli*
56. Carapace rather lengthened (about as in *P. vittata*, etc.). Median light band broad with edges narrowing posteriorly. Lateral bands continuously broad; separated from the edge of carapace by a narrow dark band. Anterior pockets of epigynum as in Figure 41. The epigynum is reddish yellow made up of thin cuticle that easily yields under slight pressure .... *P. nigriceps*
— Carapace not particularly long. Lateral light bands always narrower than the dark ones 57
57. The anterior pockets are far apart and placed on the anterior external corner of epigynum. Median septum more or less dilated posteriorly. Genital depressions ear-shaped or somewhat triangular (*P. riparia* group) 58
— Anterior pockets always close to each other, sometimes touching, sometimes separated by the median septum 61
58. Genital depressions ear-shaped. Septum dilated posteriorly (Fig. 45) .... *P. riparia*
— Genital depressions triangular. Septum posteriorly rounded 59
59. A straight line across the center of the anterior pockets would intersect the median septum at about its middle point (Fig. 51) .... *P. pullata*
— A straight line across the center of the anterior pockets would intersect the septum much more anteriorly or would not touch it at all 60
60. If the septum is so intersected, it is at the level of the anterior quarter. Septum rather broad (Fig. 48) .... *P. femoralis*
— If the line crosses the septum it does so just at the septum's anterior edge or does not cross it at all (Fig. 55) .... *P. prativaga*
61. Median light band of carapace not distinct, dilated behind the posterior eyes and at

level of the median furrow. Generally it is made up of two oval spots divided by a thin line, followed by a dark rhomboidal spot, and then in the thoracic region a more or less distinct light band, never branched. Lateral bands evident or not, sometimes continuous, sometimes broken. Spinnerets dark brown, at least the lower pair. Edge of the anterior pockets united, more or less bent _____ 62

— Median light band of carapace almost always distinct, and at least in the thoracic region, dilated, branched or spindle shaped. If not very clear, then the lateral bands are clear and evident and clearly broken. Spinnerets light. Edge of the anterior pockets different _____ 66

62. Lips of the epigynum parallel, more than half the length of epigynum, then diverging posteriorly (compare Figs. 18, 25, 28) _____ 63

— Lips of epigynum immediately diverging or subparallel on the anterior fifth of the length of epigynum _____ 65

63. The septum starts under the anterior pockets and is enlarged twice, as in Figure 28 _____ *P. sordidata*

— The septum does not start under the anterior pocket and is enlarged posteriorly only once _____ 64

64. The anterior portion of the epigynal depression, containing the pedunculus of the septum, is much longer than the second portion containing the transverse portion of septum (Fig. 25). Lateral bands of carapace distinct _____ *P. paludicola*

— Anterior portion of the epigynal depression not longer, or barely longer, than the second portion (Fig. 18). Lateral bands of carapace very obscure _____ *P. giebeli*
(and *P. eiseni luciae?*)

65. Lateral bands of carapace distinct, continuous (Fig. 33). Anterior pocket of epigynum wide; lips of genital depression diverging at once (Fig. 32) _____ *P. lapponica*

— Lateral bands of carapace obscure. Anterior pocket of epigynum narrow. Lips of genital depression subparallel at least for a short distance (Fig. 38) _____ *P. ferruginea*

66. Median light band of carapace wide with more or less parallel edges, or spindle-shaped, sometimes anteriorly ending as a diamond shape, but never dilated anteriorly and on the thoracic region. Median

band generally clear-cut _____ 67

— Median light band more or less clear-cut, dilated behind the posterior eyes and at level of the thoracic furrow; sometimes clear only on the thoracic region, sometimes rather obscure _____ 70

67. Median light band of carapace wide with subparallel edges, covered with white pubescence. Lateral bands narrow, rather obscure (Fig. 59). Epigynum as in Figure 58, anchor-shaped. Species rather common, easily seen running on dried leaves in woods _____ *P. lugubris*

— Median light band spindle-shaped, or ending with a little diamond-shaped enlargement _____ 68

68. Lateral bands of carapace broken _____ 69

— Lateral bands of carapace continuous though not very clear (Fig. 148). Body color brown or greenish brown. Abdominal pattern yellow, distinct. Epigynum as in Figure 149. Lips of the anterior part of genital depression not parallel ____ *P. cribrata*

69. Body color reddish. Carapace as in Figure 146. Abdominal pattern reddish brown. Epigynum as in Figure 147. Lips of the anterior part of genital depression parallel. Very common species ____ *P. proxima*

— Body color red brown. Median band of carapace not particularly evident. Epigynum as in Figure 127 _____ *P. aenigmatica*

70. Lateral bands of carapace continuous, sometimes deeply serrated _____ 71

— Lateral bands broken _____ 73

71. Median band of carapace greatly branched in the thoracic region. Lateral bands clear but deeply serrated on the external edges _____ 72

— Median band obscure, sometimes distinct only posteriorly (Fig. 141). Lateral bands yellow, covered with black hairs and spots. Epigynum as in Figure 142. Species inhabits only the border of salt-marshes _____ *P. luctinosa*

72. Epigynum as in Figure 122. Species of eastern Alps and eastern Europe through Caucasus _____ *P. nebulosa*

— Epigynum as in Figure 126. Occurs in Sardinia and Abyssinia _____ *P. naevia*

73. Anterior pockets single. Anterior portion of septum dilated as a yellow semilunar piece, then constricted (pedunculus) and then again dilated on the transverse por-

tion of septum (Fig. 62) ..... *P. amentata*

– Anterior pockets single or double. Septum triangular in shape, more or less long, pedunculate anteriorly 74

74. Anterior pockets clearly divided by pedunculus of septum; the edges of the septum continue as edges of the anterior pockets. Septum long, pedunculate, plain or depressed on the median portion 75

– Anterior pockets more or less close. The edges of the pedunculus of septum do not continue as edges of the pockets 77

75. Septum flat. Median light band of carapace not very clear 76

– Septum medially depressed. Posteriorly and laterally to the septum are very distinct posterior pockets, subcircular and dark brown. Median light band of carapace limited to two little spots on the cephalic region and to a branched band on the thoracic one (Fig. 137). Lateral bands clearly broken. [Epigynum (Fig. 138) like that of *P. luctinosa*] .... *P. italica*

76. Color dark brown, but all body covered with gray hairs. Leg annulations pale. Total length of body, 6–7.5 mm. Length of septum, 0.5 mm. Lives on plains to 1400 m (Figs. 130, 131) .... *P. wagleri*

– Color of carapace chocolate brown, with sparse gray pubescence. Legs reddish yellow, clearly annulated. Total body length, 7.8–9.5 mm. Length of septum, 0.75 mm. Lives on the mountains above 1400 m height (Fig. 134) ..... *P. saturatior*

77. The septum does not entirely fill genital depression which is divided into anterior and posterior, the anterior light and flat, the posterior half-filled. (The shape of septum is rather variable.) Very common species (Fig. 151) .... *P. hortensis*

– The septum nearly fills the entire genital depression and has the appearance of a triangular plate 78

78. Median light band strongly dilated behind posterior eyes, yellow and very distinct. Lateral bands evident. Body color yellow-brown to greenish 73

– Median and lateral bands reddish, not distinct. Median band often only in the thoracic region. General body color dark chocolate brown. Epigynum as in Figure 66 .... *P. morosa*

79. The points of basal spines of anterior metatarsus hardly reach, or extend only a

little beyond the base of median pair. Epigynum as in Figure 144 .... *P. strigillata*

– The points of the basal spines of anterior metatarsus extend beyond the basal half of the median pair. Epigynum as in Figure 145 .... *P. pseudostrigillata*

Pardosa mixta (Kulczynski)

Figures 80–81, 93, 104–106

Lycosa mixta Kulczynski, 1887, Rozpr. spraw. wudz. mat. przyrod. Akad. Umiej. 16: 299, pl. 5, figs. 11, 12, ♂ ♀. Male and female syntypes from southern Tyrol, "Schlern Mountain," probably in Budapest Museum.

Pardosa mixta,—Roewer, 1954, Katalog der Araneae, 2a: 167. Bonnet, 1958, Bibliographia Araneorum, 2: 3388.

Description. Carapace brown. Median band pointed in front, in the male often faint anteriorly. Lateral bands continuous, about as broad as the median one; separated from the carapace margins by a narrow dark band, then by another thin light band (Fig. 93). Legs yellow-brown. Femora with dorsal longitudinal dark marks; the other segments with indistinct rings, clearer on posterior legs. Tarsus, metatarsus and part of tibia of male with very long laterally and forwardly directed hairs (Fig. 106). Abdomen brown-red. Male palpus as in Figures 104, 105. Epigynum as in Figures 80, 81. Septum a little broader than long. Posterior angles more or less blunt, wrinkled, and sometimes prominent.

Remarks. The male cannot be mistaken for any other species because of the long hairs on the three first segments of the first leg. The females are distinct from *P. blanda* (and *albata*?) and *P. palustris* by the shape of the epigynum and particularly by the different shape of the edge of the anterior pockets. The females of *P. mixta*, *P. agricola* and *P. torrentum* differ in the carapace pattern; *P. mixta* differs from *P. monticola* by having the septum broader than long (in *P. monticola* it is longer than broad or as long as broad). The lateral light bands are generally a little broader than the median bands in *P. agrestis* (*pseudomonticola*

Simon) while they are about equal in *P. mixta*.

Ecology. *Pardosa mixta* is mentioned mostly from Alps at high altitudes (about 2000–2500 m). It seems to like open wet meadows. The record from the Apennines (Monte Cimone, 2163 m) is not surprising in view of the glacial history.

Specimens examined from Italy. *Piemonte.* Alpi Pennine: Colle d'Olen, 2865 m (Gnecco, MSNG). *Valle d'Aosta.* Valsavaranche (Festa, MSNF); Gressoney la Trinité: Lake Gabiet, 2339 m, 22.VIII.1958. *Trentino.* Dolomiti (SMF). *Friuli-Venezia Giulia.* Carnia (Di Caporiacco, MSNF). *Toscana.* Appennino Tosco Emiliano: Mt. Cimone (MSNF).

Specimens examined from outside Italy. *Switzerland.* Canton Ticino (Pavesi, MSNG). *Austria.* Tyrol: Ober-Gurgl im Ötztal, 2000 m, June 1958 (Levi, MCZ).

General distribution. Switzerland, Italy, Austria, Carpathians, Yugoslavia.

Pardosa palustris (Linnaeus)

Figures 84–85, 91, 102–103

Araneae palustris Linnaeus, 1758, Systema Naturae, 10 ed., p. 623. Holotype from Sweden lost.
Lycosa herbigrada Blackwall, 1857, Ann. Mag. Nat. Hist., (2)20: 285. Female syntypes from Isle of Portland, Dorset, England, in British Museum, London.
Pardosa herbigrada,—Roewer, 1954, Katalog der Araneae, 2a: 163. Bonnet, 1958, Bibliographia Araneorum, 2: 3373.
Pardosa palustris,—Roewer, 1954, *op. cit.*, 2a: 177. Bonnet, 1958, *op. cit.*, 2: 3402.

Description. The carapace patterns are not very different from those of *P. monticola*. In several specimens the light lateral bands are separated from the carapace margins by a continuous dark band, but specimens can be found in which the outer dark bands are reduced (Fig. 91). Some specimens have different carapace patterns and often have been regarded as belonging to a different species, e.g. *P. herbigrada* (Blackwall). Such specimens have never been recorded in Italy (compare Tongiorgi, 1965). Legs yellow with more or less distinct annulations. Femora with dark blotches dorsally. Terminal apophysis of the male palpus is a broad, slightly curved, more or less sharp and jagged lamina. It is very characteristic and unique to this species (Figs. 102, 103). Epigynum as in Figures 84, 85. Septum much broader than long, posterior angles obtuse, often prominent and wrinkled. A deep groove extends about two-thirds of the septum's length. Edge of the anterior pockets very characteristic. Color rather variable: posterior angles generally dark brown-red, but plate usually evenly colored, or only one side darkened. Because of the great variability of the epigynum, I have drawn only two examples.

Remarks. The peculiar structure of the terminal apophysis of the palpus distinguishes the males of *P. palustris* from those of the other species. The females cannot be mistaken for any other species, as the shape of the epigynum is very characteristic, and though it may vary greatly, it always permits reliable diagnosis. The edge of the anterior pockets has the same structure only in *P. blanda* (and *P. albata*?). The only closely related species is *P. mixta*, which often has posterior angles of the septum similarly wrinkled and prominent, but is distinguished from *P. palustris* by the edges of the anterior pockets and by having the sides of the septum generally more parallel.

Ecology. The species is widespread, especially in cold climates. It lives on mountains mostly in open and rather dry places, i.e., meadows, pastures, heaths.

Specimens examined from Italy. *Piemonte.* Alpi Pennine: Colle d'Olen, 2865 m (Gnecco, MSNG); Macugnaga, 1600 m, Val Anzasca, 30.VII.1961. Torino: Pratiglione Ivrea, (MSNF). *Valle d'Aosta.* Gressoney la Trinité, 1627 m, 20.VIII.1958; Capanna Morgenrot, 1800 m, 20.VIII.1958; Capanna S. Anna, 2170 m, 27.VIII.1958. Gressoney St. Jean, 1385 m, 23.VIII.1958. *Emilia-Romagna.* Forlì: Campigna, 20.VII.1942 (Zangheri, CZ). *Toscana.* Lucca: Orecchiella, S. Romano, 1220 m, 4.VIII.1965.

General distribution. Palearctic, Alaska.

Pardosa agricola (Thorell)
Figures 77–79, 98, 107–108

Lycosa arenaria C. L. Koch, 1834, *in* Panzer, Faunae Insectorum Germaniae, Heft 123, pls. 15–16. Syntypes from the Danube bank near Regensburg, Germany, probably in the British Museum, London. Name preoccupied by *L. arenaria* Savigny and Audouin, 1825.
Lycosa agricola Thorell, 1856, Nova Acta Reg. Soc. Sci. Upsala, (3) 2 (1): 171.   New name.
Pardosa agricola,—Roewer, 1954, Katalog der Araneae, 2a: 157.   Bonnet, 1958, Bibliographia Araneorum, 2: 3348.

Description.   Carapace dark brown. Light median band dilated anteriorly, sometimes branched on the thoracic region (Fig. 98). On several specimens the median band is not broader than the lateral ones, and on some the anterior enlargement is not very evident. Lateral bands very clearly broken. Occasionally the posterior spots merge. Abdomen very dark with brown-red pattern. Legs yellow, very distinctly annulated. Male palpus with two teeth on the terminal apophysis. Tegular apophysis long and blunt at the end (Figs. 107, 108). The female has the genital plate about as long as broad. Lateral sides very sinuous. Edge of the anterior pockets as in Figures 77–79. (Owing to the great variability, *P. agricola* can often be mistaken for *P. agrestis* and *P. torrentum.*)

Remarks.   The male is easily distinguished from other species by the two-toothed terminal apophysis. The females can be confused with *P. torrentum, P. agrestis (pseudoagricola* Dahl); however, the carapace pattern distinguishes *P. agricola* from all others. *Pardosa agrestis* and *P. torrentum* have the genital plate broader than long, while *P. agricola* generally has it as long as broad. The lateral sides of the genital plate are very sinuous, and the edges of the anterior pockets are furthermore useful for distinguishing it from *P. agrestis.* The abdominal pattern seems useful for distinguishing between *P. agricola* and *P. torrentum: P. torrentum* generally has a yellow or yellow-red abdominal pattern, which is always lighter than that of *P. agricola.*

Ecology.   According to Dahl and Dahl (1927, pp. 52, 53) and Locket and Millidge (1951, p. 255), *P. agricola* prefers open sandy or stone banks of lakes and watercourses. It does not seem to reach high altitudes.

Illustrations were made from Finnish specimens loaned by P. Palmgren and F. Papi.

Specimens examined from Italy.   None, although there are numerous literature records.

General distribution.   Europe, Iran, Asia, Siberia. It is probable that specimens of *P. torrentum* have sometimes been mistaken for *P. agricola.* At least *P. agricola* seems a more common species in northern than in southern Europe.

Pardosa torrentum Simon
Figures 86–87, 99, 109–110

Pardosa torrentum Simon, 1876, Les Arachnides de France, 3: 313, pl. 13, fig. 26, ♀. Female and male syntypes from Lautaret, Briançon, in the Muséum National d'Histoire Naturelle, Paris.   Roewer, 1954, Katalog der Araneae, 2a: 174.   Bonnet, 1958, Bibliographia Araneorum, 2: 3426.

Description.   Carapace dark brown. Some specimens collected on the plain near Pisa and near Barletta are lighter yellow-brown. Median band wide, dilated anteriorly, sometimes starred in the thoracic region (Fig. 99). Lateral bands broken into three or four spots, not always so light as the median band, and often very faint in the males. Legs yellow-brown. Femora with dorsal brown marks, the other segments (except tarsi) annulated. Annulations always distinct but less so than in *P. agricola.*

Abdomen dark brown, almost black. Anterior median stripe brownish, bordered with black anteriorly, flanked and followed by bright yellow-red pattern. The light spots generally flanked by a purplish or black area. Femur and patella of male palpus clothed with white hairs (Figs. 109, 110). Epigynum as in Figures 86, 87. Sep-

tum broader than long, rarely as broad as long.

Remarks. The male is distinguished from *P. agricola* and *P. agrestis* (*pseudoagricola* Dahl) by the different shape of the terminal apophysis, from all other species by the carapace markings. To separate the females of *P. torrentum* from those of *P. agricola* and *P. agrestis* is very difficult. It seems that the abdominal pattern is lighter in *P. torrentum*, while in both other species the abdomen is generally brown-red, the pattern not greatly contrasting against the background. The legs of *P. agricola* are clearly annulated, less so in *P. torrentum*, and often only scarcely annulated in *P. agrestis*. The genital plate is generally broader than long in *P. torrentum* and *P. agrestis*, while it is as long as broad in *P. agricola*. The carapace markings set this species apart from the remaining species of the *monticola* group.

Ecology. This species lives in the mountains as well as on the plains. I found some specimens (male and female) in countries near the sea. It seems to prefer open sandy places with scant vegetation, or meadows near streams and rivers.

In Italy this species seems more common than *P. agricola*, and many erroneous citations of this last species should probably be referred to *P. torrentum*.

Specimens examined from Italy. Piemonte. Alessandria: Casale Monferrato (MSNG) ♀ ♀ ♂ ♂. *Toscana.* Pisa: Caprona, 5.VI.1958, 1 ♀; IV.1962, 1 ♂ 1 ♀. *Puglia.* Bari: Barletta, 23.VI.1961, 2 ♀ ♀.

General distribution. France, Switzerland, Tyrol, Italy, Hungary, Pyrenees.

Pardosa agrestis (Westring)
Figures 72–74, 95–97, 100–101

Lycosa agrestis Westring, 1861, Göteborg. Kongl. Vet. Handl., 7: 480. Female holotype from Sweden lost.

Pardosa agrestis,—Roewer, 1954, Katalog der Araneae, 2a: 156. Bonnet, 1958, Bibliographia Araneorum, 2: 3346.

Description. Carapace dark brown. Median and lateral bands are highly variable,

but three principal types are found: one has the median band anteriorly dilated and the lateral bands continuous (Fig. 95). Another type has the median band anteriorly dilated but the lateral bands broken (*pseudoagricola* Dahl) (Fig. 97). The third type has the median band pointed in front and the lateral bands continuous (*pseudomonticola* Simon) (Fig. 96). Legs light. Annulations more or less clear. The dark marks on dorsal side of femora may reach to ventral side. Male palpus as in Figures 100, 101. Terminal apophysis without any projecting tooth. Epigynum highly variable. Septum broader than long. Edge of the anterior pockets generally as in Figures 72–74.

Remarks. The lack of projecting teeth on the terminal apophysis distinguishes the male of this species from all others. The females are easily distinguished when the carapace pattern is as evident as in Figure 95. Otherwise they are very hard to identify. *Pardosa agrestis*, with the median band anteriorly pointed and lateral bands continuous (*pseudomonticola* Simon), is distinguished from *P. blanda* and from *P. palustris* by the different shape of the edge of the anterior pockets (compare Figs. 84, 85, 88, 89); from *P. mixta* by having the lateral bands a little broader (perhaps) than the median one, and also the epigyna of the two species are rather different. *Pardosa monticola* has the genital plate at least as long as broad while *Pardosa agrestis* has the genital plate broader than long (compare Fig. 83). The specimens having the carapace pattern as in Figure 97 (*P. agrestis pseudoagricola* Dahl) resemble *P. agricola* and *P. torrentum*. *Pardosa agricola* has the septum about as long as broad with lateral sides generally more sinuous. The legs, moreover, are very distinctly annulated. The lighter abdominal pattern of *P. torrentum* seems to me the best character for distinguishing this species from *P. agrestis*.

Ecology. According to several authors this species lives in the mountains above 2000 m as well as on the plain or near the

sea and seems to prefer open dry places or fields.

Specimens examined from Italy. Piemonte. Lago Maggiore: Astona (SMF). *Veneto.* Verona: Caprino Veronese (MSNF). *Toscana.* Lucca: Borgo a Mozzano, 31.III. 1957; Capanne di Sillano, 1100 m, 4.VII. 1965.

General distribution. Europe.

Pardosa monticola (Clerck)

Figures 82–83, 92, 94, 111–114

Araneus monticola Clerck, 1758, Aranei Svecici, p. 91, pl. 4, fig. 5, ♂ ♀. Types from Sweden probably lost.
Pardosa monticola,—Roewer, 1954, Katalog der Araneae, 2a: 167. Bonnet, 1958, Bibliographia Araneorum, 2: 3390.

Description. Carapace brown. Median light band pointed anteriorly. Lateral bands continuous and extending to the clypeus (Fig. 94). Sides of the head sometimes darkened. Lateral bands slightly broader than the median one. Lateral bands separated from carapace margins by a single dark streak (compare *P. mixta*, Fig. 93). Legs light yellow, spotted on upper side, often annulated, especially third and fourth tibiae and metatarsi. Male palpus as in Figures 111, 112, terminal apophysis with a little tooth, clearly shorter than in *P. blanda, P. albata* and *P. torrentum.* Tegular apophysis long and rather sharp. Palpus clothed with black hairs only. Epigynum as in Figure 83. Septum generally longer than broad (but sometimes as long as broad). Median groove limited to the anterior half. The posterior part of the genital plate slightly raised in the middle.

Remarks. The male of *P. monticola* is distinguished from those of *P. blanda, P. albata* and *P. torrentum* by the absence of white hairs on the palpus. From *P. torrentum* it also differs by the carapace pattern. From all the other species it differs in the shape of the terminal apophysis. The female of *P. monticola* differs from those of *P. palustris, P. blanda* (and *P. albata*?) by

having the genital plate at least as long as broad. *Pardosa monticola* differs from *P. mixta* in carapace pattern and by having the posterior angles of the plate less blunt and wrinkled (compare Figs. 80, 81). It differs very little from *P. agrestis* (*pseudomonticola* Simon), which has the septum broader than long.

On Sila Mountain (Calabria, southern Italy) near the shores of Arvo and Cecita lakes (F. Papi, August 1958) and on the slopes of Monte Pollino 1800 m (E. Mayr, May 1957), there lives a population of *P. monticola* the males of which have the tegular apophysis shorter and not so sharply pointed. Both males and females are slightly smaller. These specimens do not seem to me to be *P. monticola minima* Simon (Figs. 82, 92, 113, 114). (1 ♂ 1 ♀ are deposited in MSNG.)

In the following table I report the measurements of twelve female specimens of *P. monticola* from Sila and ten specimens collected in different countries of Europe (Italy, Germany, France, England). For each group of specimens I have given the lowest measurement (min.), the highest (max.), and the mean value of the group. All measurements are in mm.

	LENGTH OF CARAPACE		
	Min.	Max.	Mean
P. monticola	2.31	2.80	2.56
P. monticola from Sila	1.98	2.67	2.42

	LENGTH OF PLATE		
	Min.	Max.	Mean
P. monticola	0.46	0.50	0.47
P. monticola from Sila	0.36	0.50	0.43

	WIDTH OF PLATE		
	Min.	Max.	Mean
P. monticola	0.43	0.50	0.45
P. monticola from Sila	0.33	0.48	0.42

Ecology. This species lives on the mountains as well as on the plains, on the mountain-grassland as well as on dry, open ground heaths near the sea. According to de Lessert (1910, p. 511) and my own observations, this species does not seem, at least not in the Alps, to reach considerable

altitudes. Above 2000 m it is replaced by *P. mixta*.

Specimens examined from Italy. Veneto. (Canestrini, IZUP). *Friuli-Venezia Giulia.* Carnia (Di Caporiacco, MSNF). *Liguria.* Genova (Frey-Gessner, MSNG). *Toscana.* Firenze: Londa 1000–1200 m; Arezzo: Mt. Falterona 1650 m (Di Caporiacco, MSNF); Lucca: Orecchiella, S. Romano, 1220 m. *Calabria.* Sila Grande, 1450 m, 18.V. 1957 (E. Mayr, MCZ); Mt. Pollino, 1800 m, 14.V. 1957 (E. Mayr, MCZ); Lake Cecita, Lake Arvo, Sila, 8.VIII.1958 (F. Papi); Cosenza: Silvana Manzio, 24.VI.1960 (S. Ruffo, MSNV).

Specimens examined from outside Italy. France. Mt. Canigon, southern France (SMF). Corsica: Vizzavona (SMF). *Switzerland.* Vaud: Montreux, 400–1100 m (Levi, MCZ). *Austria.* Tyrol: Seefeld 1200 m, Karwendel Mts. (Levi, MCZ). *Germany.* Nieder Sachsen: Göttingen (Levi, MCZ).

General distribution. Europe, Afghanistan, Siberia, China.

Pardosa blanda (C. L. Koch)
Figures 88–90, 115–116

Lycosa blanda C. L. Koch, 1833, Arachniden. *In* Panzer, Faunae Insectorum Germaniae initia. Heft 120, pl. 24. Male holotype and female paratype from near Nassfelde, Salzburg, Austria, probably in British Museum, London.

Pardosa blanda,—Roewer, 1954, Katalog der Araneae, 2a: 160. Bonnet, 1958, Bibliographia Araneorum, 2: 3360.

Description. Carapace dark brown. Median light band narrow, spindle-shaped; occasionally slightly enlarged at the anterior end and at the level of the thoracic furrow, and here sometimes faintly branched. Median band clothed with white pubescence. A narrow line made up of light pubescence only may continue between the posterior median eyes. Lateral bands yellow. Often two very thin dark lines divide each band into three light spots (Fig. 90). Lateral bands about as broad as the median one. Between the lateral band and the carapace margin there is a dark brown band narrower than the light one. The lateral bands do not continue forward on the clypeus but stop on the sides of the head.

Abdomen with reddish pattern on almost black background. Ventral side thickly clothed with white pubescence. Legs rather darkened. Femora uniform or with dark brown spots on dorsal side. Tibia and metatarsi annulated, especially on the posterior legs. Tarsi uniform. Males with darker and less clearly annulated legs. Male palpus (Figs. 115, 116) with distal end of femur and patella clothed with white hairs. Terminal apophysis forms a strong tooth. Epignal septum broader than long, not greatly variable in shape. Edge of the anterior pockets as in Figures 88, 89.

Remarks. The male is very close to *P. albata, P. monticola* and *P. torrentum*, especially concerning the terminal apophysis of the palpus. It is distinguished from *P. monticola* by the bigger terminal apophysis and the thicker tegular apophysis. Further, *P. monticola* does not have white hairs on the palpus. *Pardosa albata* has the palpus entirely clothed with white hairs. *Pardosa torrentum* has a different carapace pattern. The females are distinguished from those of *P. monticola* and *P. mixta* by the edge of the anterior pockets (compare Figs. 80, 81, 83). *Pardosa blanda* is distinguished from *P. palustris* by the shape of the plate. It is easily distinguished from all other species by the epignum and the carapace pattern. It may sometimes be difficult to separate *P. blanda* from *P. agrestis* (*pseudomonticola* Simon). The latter has the lateral bands continuous around the head while in *P. blanda* these are often broken off anteriorly on the sides of the head.

Ecology. Pardosa blanda lives in mountainous zones between 1000 m and 3000 m, but is especially frequent at about 2000 m. It seems to me that the southern point recorded for this species is Varco of Mt. Pollino (about 2000 m) in the south of Italy (Simon, 1882).

Specimens examined from Italy. Piemonte. Torino: Pratiglione Ivrea (Cavanna, MSNF); Alpi Pennine: Colle d'Olen, 2865

m (Gnecco, MSNG); Macugnaga: Alpe Cicerwald, 1200–1600 m, Val Anzasca. *Valle d'Aosta.* Valsavaranche (Festa, MSNF); Gressoney la Trinité: S. Anna, 2170 m; Lake Gabiet 2339 m; Gressoney la Trinité: 1627 m. *Trentino.* Bolzano (SMF). *Friuli-Venezia Giulia.* Carnia (Di Caporiacco, MSNF) (Di Caporiacco recorded this species under several names: *P. torrentum, lugubris, agricola, palustris, monticola, nigra*). *Emilia-Romagna.* Forlì: Campigna, 1.VII.1924; Piancancelli, 22.VII.1925 (Zangheri, CZ). Campigna, Mt. Falco (Di Caporiacco, CZ); Modena (SMF). *Toscana.* Mt. Falterona, 1500–1650 m (Di Caporiacco, MSNF); Arezzo: Colle del Castagno, 1200 m, Mt. Acuti, 1428 m (Di Caporiacco, MSNF); Lucca: Capanne di Sillano, 1100 m. *Marche-Umbria.* Pesaro: Avellana (MSNF); Sibillini Mts., several localities (Ruffo, MSNV). *Lazio.* Montecassino: Mt. Cairo, 1669 m (Cavanna, MSNF). *Abruzzi-Molise.* Pescara: Caramanico (MSNF); Cima Matese, Mts. of Matese (Cavanna, MSNF). *Abruzzi.* (SMF); Sulmona: Mt. Morrone (Cavanna, MSNF); Campitella Matese, 16. VI.1962 (Ruffo, MSNV). *Campania.* Picentini Mts. (Ruffo, MSNV).

Specimens examined from outside Italy. Yugoslavia. Istria: Mt. Ucka, 1400 m (Levi, MCZ). *Austria.* Tyrol: Ober-Gurgl im Ötztal, 2000 m (Levi, MCZ); Karwendel Mts., 1200 m (Levi, MCZ).

General distribution. France, Germany, Switzerland, Italy, Czechoslovakia, Austria, Poland, Hungary.

Pardosa albata (L. Koch)
Figures 117–118

Lycosa albata L. Koch, 1870, Jahrb. k.k. Gelehr. Gesell. Krakau, 41: 36. Male and female syntypes from the Tatra Mts. and Bukowina [Carpathian Mts.] probably in the Berlin Museum.

Pardosops albatula Roewer, 1954, Katalog der Araneae, 2a: 196.

Pardosa albata,—Bonnet, 1958, Bibliographia Araneorum, 2: 3350.

Description. Of this species I could examine only two male specimens in the col-

lection of spiders from Carnia studied by Di Caporiacco (1922, 1927), and preserved at the Museum of Natural History of Florence. The only differences from *P. blanda* are that the palpus is covered with white pubescence from the base of the femur to about the middle of the tarsus, and that the tegular apophysis (Figs. 117, 118) has a slightly different shape.

To separate the females of the two species the description by Koch and the distinctive characters for *L. cursoria* (*P. blanda*) (Koch, 1870, p. 42) are not sufficient.

Ecology. Species of the mountainous districts of southern and eastern Europe.

Italian distribution. Carnia.

General distribution. Germany, Hungary, Poland, Austria, Siberia, Italy, Carpathians, Balkans, Transylvania.

Pardosa saltuaria (L. Koch)
Figures 67–71

Lycosa saltuaria L. Koch, 1870. Jahrb. k.k. Gelehr. Gesell. Krakau, 41: 38. Female syntypes from the Tatra Mts. and Bukowina, probably in the Berlin Museum.

Pardosa saltuaria,—Roewer, 1954, Katalog der Araneae, 2a: 178. Bonnet, 1958, Bibliographia Araneorum, 2: 3420.

Pardosa oreophila Simon, 1937, Les Arachnides de France, 6: 1071, fig. 1668, ♀. Female holotype from the French Alps in the Muséum National d'Histoire Naturelle, Paris, examined. NEW SYNONYMY.

Description. Carapace dark brown. Light median band yellow, narrow, and spindle-shaped. Lateral bands yellow, rather wide and continuous. Each lateral band includes, near the edge of the carapace, a narrow brown band made up of spots that approach each other (Fig. 70). Carapace of male darker; median and lateral bands reddish yellow. The median one spindle-shaped, not very clear-cut; the lateral bands are narrow and separated from the edge of the carapace by a dark band and a thin light line. Abdomen reddish brown. Lower spinnerets of female are brown. The male has all black spinnerets. Legs of female reddish yellow with annulations; tibia and meta-

tarsus of fourth pair brown. Male with yellow legs, only femora darkened on upper side.

Remarks. Though often included in the *Pardosa monticola* group, *P. saltuaria* is different from all species of this group. Among Italian *Pardosa*, males of other species also have black spinnerets (*P. bifasciata, P. schenkeli, P. lapponica*), but *P. saltuaria* differs by the shape of tegular apophysis (Figs. 67, 68). The epigynum of *P. saltuaria* (Fig. 69), though similar to that of species of the *P. monticola* group, is easily distinguishable.

I examined the female holotype of *P. oreophila* Simon (Fig. 71), and find it to be exactly like *P. saltuaria*. The proximal spines of the anterior metatarsus exceed the bases of median ones by about one-third, and the epigynum is smaller, but those characters are not sufficient to keep *P. oreophila* a separate species.

Ecology. This is a species of the Alps, on meadows and open places, from 1000 m as high as 2700 m. It is a common species often misidentified by Di Caporiacco.

Specimens examined from Italy. Friuli-Venezia Giulia. Carnia (Di Caporiacco, MSNF). South Tyrol, Dolomiti (SMF).

Specimens examined from outside Italy. Austria. Tyrol: Ober-Gurgl (Levi, MCZ).

General distribution. Arctic regions, central and southern European mountains, from France to the Balkans.

Pardosa nigra (C. L. Koch)
Figures 123–125

Lycosa nigra C. L. Koch, 1834, Arachniden, *in* Panzer, Faunae Insectorum Germaniae initia, Heft 122, pls. 13–14, ♀ ♂. Male and female syntypes from a brook of the Nassfelder Alps, Salzburg, Austria, probably in the British Museum, London.

Lycosa celeris Thorell, 1875, Tijdschr. Ent., 18: 106. Two female syntypes from northern Italy, probably lost. (They are not in the Stockholm or Genoa museums, but might have been in Padua with the Canestrini collection.) NEW SYNONYMY.

Acantholycosa nigra,—Roewer, 1954, Katalog der Araneae, 2a: 151.

Pardosa celeris,—Roewer, 1954, *op. cit.,* 2a: 160. Bonnet, 1958, Bibliographia Araneorum, 2: 3363.

Pardosa nigra,—Bonnet, 1958, *op. cit.,* 2: 3395.

Description. Carapace dark brown, a little lighter in the thoracic region. Lateral light bands absent, or represented by two or three lighter spots, often more evident at level of thoracic furrow. General body color reddish to very dark brown. Abdomen black with brick red pattern. Reddish on ventral side. Both male and female with red-brown legs. Femora darker, almost black. Tarsi reddish yellow, or lighter than other segments. Tibiae of first pair ventrally with four pairs of spines, as well as an apical pair of shorter ones, rarely only three pairs. Male palpus, Figures 123, 124. Epigynum as in Figure 125.

Remarks. In having four pairs of spines on the ventral side of the first tibia, *P. nigra* differs from all other Italian *Pardosa*. Some authors regard this species as belonging to the genus *Acantholycosa* Dahl (Roewer, 1954, p. 152; Di Caporiacco, 1940; Denis, 1963). Since morphological characters of genitalia, especially those of the male palpus, are quite comparable with those of other *Pardosa*, but are quite different in *Acantholycosa*, I shall consider *P. nigra* as a species of *Pardosa*. It seems to me, moreover, that the true *Acantholycosa* have five or more pairs of spines on the ventral sides of the first tibia. Of *Pardosa celeris* I examined four immature specimens (Thorell collection in NRS; type species lost?). They agreed with young specimens of *P. nigra* with which I compared them. They have only four pairs of spines on the first tibia (compare Thorell, 1875, p. 146). Thorell himself indicated that the epigynum is like that of *P. nigra*. Also, the annulation of the legs described by Thorell for *L. celeris* is not exceptional; one finds these characters in lighter specimens of *P. nigra*. *Pardosa celeris* (Thorell) thus is a synonym of *P. nigra* (C. L. Koch).

Ecology. This species lives from sea level up to 3000 m. In mountain regions it

prefers stony places near the snow line. Specimens mature in June and August.

Specimens examined from Italy. Piemonte. Torino: Pratiglione Ivrea, 3 ♂ ♂, 21.VIII.1879 (MSNF). *Valle d'Aosta.* Aosta: Valsavaranche (Festa, MSNF); Gressoney St. Jean, 1385 m (Gnecco, MSNG). *Lombardia.* Valsesia, 1 ♀ (Piccone, 1871, MSNG). *Trentino-Alto Adige.* South Tyrol (Dolomiti) 1 ♂ 1 ♀ (SMF). *Friuli-Venezia Giulia.* Carnia (Di Caporiacco, MSNF). *Veneto.* 1 ♀ (Canestrini, IZUP). *Liguria.* Chiavari, 1 ♀ (SMF). *Alpi.* 3 ♀ ♀ 1 ♂ (MCZ).

Specimens examined from outside Italy. Switzerland. Canton Ticino, 1 ♀ (Pavesi, MSNG). *Crete.* Canea (Roewer, SMF).

General distribution. France, Germany to Russia, Italy, Balkans, Crete.

Pardosa giebeli (Pavesi)
Figures 15–18

Lycosa giebelii Pavesi, 1873, Ann. Mus. civ. Stor. nat. Genova, 4: 164, figs. 7–9, ♂ ♀. Female, male syntypes from Monte Fibbia and Valle di Fortunei, 2500 m [S. Gottard, Lepontine Alps, Switzerland], in the Museo Civico di Storia Naturale, Genoa, examined.

Pardosa giebeli,—Roewer, 1954, Katalog der Araneae, 2a: 175. Bonnet, 1958, Bibliographia Araneorum 2: 3370.

Description. Carapace dark brown, median light band reddish yellow, more distinct in the thoracic region. At level of the median furrow it sometimes is slightly branched, and in the cephalic region, darker and often faint. The indistinct, broken lateral bands are much clearer posteriorly. Males have the carapace pattern less distinct and darker. Abdomen blackish brown with red pattern. Wide lanceolate median stripe bordered with white hairs. The other spots are confluent, resulting in a single band covering the abdomen dorsum. There are a few white hairs posteriorly. The spinnerets are dark. Legs red-brown. Femora blotched and annulated above, especially near the base, more or less uniformly darkened ventrally; other segments uniform. Male palpus (Figs. 15, 16, 17), observed from the apical end, exhibits a long and

sharpened embolus, lying on the almost transparent alveolus. Epigynum as in Figure 18.

Remarks. *Pardosa giebeli* is closely related to *P. eiseni* (Thorell), which lives in the cold regions of northern Europe and Asia, except in the Alps, where the subspecies *P. eiseni luciae* occurs. The different shape of the embolus distinguishes the males of the two species (compare Figs. 17, 21, 22). I could not examine females belonging with certainty to *P. eiseni luciae*. There are good drawings of *P. giebeli* and *P. eiseni* (= *P. arctica* Kulczynski) in the paper of Kulczynski, 1916; however, the differences in the epigyna of the two species are not as distinct as indicated by figures 69 and 70 of this author. Other species belonging to the *P. giebeli* group have been described from Palearctic and Nearctic regions. *Pardosa uintana* Gertsch, from the United States, of which I examined several specimens, is clearly distinguished from *P. giebeli* by the genitalia.

Ecology. *Pardosa giebeli* lives in the Alps to the highest altitudes. Generally it has been found on meadows between 2000 and 3000 m.

Specimens examined from outside Italy. Switzerland. (MSNG); Grundsee, 2310 m, 15.VII.1909, ♂ ♂ ♀ ♀ (MHNG); Riffelberg, 2800 m, 23.VII.1909 (MHNG). *France.* 2 ♀ ♀ (MCZ). *Austria.* Vorarlberg, VIII.1961 (Neis, SMF).

General distribution. French, Swiss, Italian Alps.

Pardosa eiseni luciae new subsp.
Figures 19–22

Type. Male holotype from Faulhorn, 2545 m, Alps, near Brig, Valais, Switzerland, in the Museum of Comparative Zoology.

Description. Carapace dark brown without bands. Abdomen black with red-brown pattern. Spinnerets black. Legs red-brown; femora annulated, tibia less so. Male palpus illustrated by Figures 19, 20, 22; the angular embolus ends as a spatula. I cannot distinguish females of this subspecies from those of *P. giebeli*. The females in the vial

with the holotype have very faint bands on the carapace, while in *P. giebeli* there is generally a median band, though not very clear; the epigyna are identical, even when cleared and observed from the dorsal side. [Compare the differences between *P. giebeli* and *P. arctica* Kulczynski (= *eiseni*) in Kulczynski 1916, pl. 15, figs. 71–72.]

Remarks. In the shape of embolus this species is without doubt much closer to *P. eiseni* than to *P. giebeli* (compare Figs. 17, 21, 22). *Pardosa giebeli* has a long, sharpened embolus; *P. eiseni eiseni* and *P. eiseni luciae* have the embolus bent almost at a right angle and broadened and flattened distally. The distal part of the embolus of the specimen I examined distinguishes *P. eiseni luciae* from *P. eiseni eiseni*. It is not surprising to find that *P. eiseni* has a boreo-alpine distribution as do some other *Pardosa* (e.g., *P. lapponica*). This record is the southernmost record of *P. eiseni*; the specimen differs slightly, and seems to be a new subspecies.

Pardosa schenkeli Lessert
Figures 12–14

Pardosa schenkeli Lessert, 1904, Rev. Suisse zool., 12: 429, pl. 6, figs. 42–44, ♀ ♂. Female, male syntypes from Arella, Valais, in the Muséum d'Histoire Naturelle, Geneva.

Lycosa calida,—Dahl and Dahl, 1927, *in* Die Tierwelt Deutschlands, 5: 38, figs. 98–102, ♂ ♀. (Not *Lycosa calida* Blackwall.)

Passiena schenkeli,—Roewer, 1954, Katalog der Araneae, 2a: 198.

Pardosa calida,—Bonnet, 1958, Bibliographia Araneorum, 2: 3362 (in part).

Description. The description of *P. bifasciata* fits this species very well. The body pattern is so similar that only genitalia can be used to distinguish *P. schenkeli* and *P. bifasciata.* Male palpus (Figs. 12, 13) has the tegular apophysis with a pointed and outwardly-directed tooth. Epigynum (Fig. 14) has the septum rather long. Connecting canals of the seminal receptacle, which show through the cuticle, have at least two coils.

Remarks. The male of *P. schenkeli* differs from that of *P. bifasciata* in the shape

of the tegular apophysis. The different structure of the anterior pockets and seminal receptacles separates the females of these species.

The synonymy of *P. schenkeli* is controversial. It seems to me that the opinion of de Lessert (1910), with which Simon (1937) agrees, should be followed. Dahl (1908), Dahl and Dahl (1927) regard this species as a synonym of *P. calida* (Blackwall), but the description of *P. calida* suits either *P. schenkeli* or *P. bifasciata* equally well. As the species described by de Lessert is clearly illustrated and identifiable, whereas we cannot say the same of *P. calida*, and whereas many of the records of *P. calida* are certain to be referred to *P. bifasciata*, it seems to me better to consider *P. schenkeli* a good species and *P. calida* a synonym of *P. bifasciata.*

The inclusion of *P. schenkeli* and *P. bifasciata* within the genus *Passiena* Thorell (Roewer, 1954, 1958, p. 162) is arbitrary. Roewer attributes to Simon the inclusion of *P. bifasciata* (and consequently of *P. schenkeli*) into the genus *Passiena*. Simon never did that; he limited himself to supposing a proximity of morphological characters of this species to his *Pardosa auberti* and to *Passiena spinicrus* Thorell (Simon, 1898, p. 355). One of the distinctive characters of *Passiena*, according to Roewer, is the presence of four pairs of spines on the ventral side of of the first tibia. *Pardosa bifasciata* and *P. schenkeli* have three pairs of spines on the ventral side of the tibiae, besides the little apical pairs. Judging by the drawings of Roewer (1958) all species belonging to *Passiena* have quite different genitalia from those placed in *Pardosa*. In *Pardosa bifasciata* and *P. schenkeli*, the genitalia are as in other *Pardosa* species.

I could examine only one female and one male of *P. schenkeli* from France (MCZ collection). The drawings were made from these specimens.

Ecology. This is a species of the Alps between 1500–2500 m. According to de Lessert (1910) it lives in the upper zone of

conifer forests and pastures. *Pardosa schenkeli* has not yet been recorded for Italy.

General distribution. Alps, Ural of Verchoturijé (Charitonov, 1926).

Pardosa bifasciata (C. L. Koch)
Figures 8–11

Lycosa bifasciata C. L. Koch, 1834. Arachniden. *In* Panzer, Fauna Insectorum Germaniae initia, Heft 125. Male and female syntypes from Germany, probably in the British Museum, London.

Passiena bifasciata,—Roewer, 1954, Katalog der Araneae, 2a: 198.

Pardosa bifasciata,—Bonnet, 1958, Bibliographia Araneorum 2: 3359.

Description. This is one of the smallest species of *Pardosa* in Italy. Carapace rather long and narrow, dark brown in color. Median light band yellow with parallel edges, extended anteriorly beyond the row of posterior eyes. Yellow, lateral bands wide, continuous. A little dark band contained within each light band near the outer edge (Fig. 11). Carapace of male reddish brown, median and lateral bands less clear. Sternum of females yellow with dark spots or with two narrow dark longitudinal bands. Dark with a light median band on males. Male with lower spinnerets black. Abdomen blackish brown. Anteriorly there is a lanceolate stripe with white pubescence and bordered with black. On each side of the lanceolate stripe is a yellowish band. The bands of the two sides joined into one reaching the spinnerets. Legs yellow, the lateral sides of femora with longitudinal black stripes. Other segments uniform. The male has the femora often more or less uniformly darkened, especially the anterior ones. Palpus as in Figures 8, 9. Epigynum (Fig. 10) has the seminal receptacles generally visible through the cuticle, and the connecting canal of each receptacle coiled once.

Remarks. The color pattern of this species distinguishes it readily from almost all other *Pardosa.* The males differ from those of *P. vittata* by lacking long hairs on the second metatarsi, females by the shape of epigynum. *Pardosa bifasciata* differs from *P. schenkeli* only by the shape of the genitalia (Figs. 12, 13, 14).

Ecology. This species is found in dry and sandy places amid grass, at low elevations or subalpine regions. Mature specimens have been collected from May to August and September.

Specimens examined from Italy. *Trentino.* Trento: Levico, 1873, 1 ♂ (Frey-Gessner, MSNG). *Friuli-Venezia Giulia.* Carnia, 2 ♀ ♀ 1 ♂ (Di Caporiacco, MSNF).

Specimens examined from outside Italy. *Switzerland.* Canton Ticino, 3 ♂ ♂ (Pavesi, MSNG). *France.* 1 ♂ 1 ♀ (mixed with *P. schenkeli*) (MCZ).

General distribution. Throughout continental Europe, Asia Minor.

Pardosa vittata (Keyserling)
Figures 1–7

Lycosa vittata Keyserling, 1863, Verhandl. zool. bot. Gesell. Wien, 13: 369, pl. 10, fig. 7, ♀. Female syntype from Dalmatia in the British Museum.

Pardosa palitans Simon, 1876, Les Arachnides de France, 3: 326, pl. 13, figs. 21, 22, ♀ ♂. Syntypes from numerous localities in southern France and Corsica, in the Muséum National d'Histoire Naturelle, Paris; 1937, *op. cit.,* 6: 1056, 1077, 1130, figs. 1625, 1627, 1675, ♀ ♂. Roewer, 1954, Katalog der Araneae, 2a: 169. Bonnet, 1958, Bibliographia Araneorum, 2: 3399. NEW SYNONYMY.

Pardosa vittata,—Roewer, 1954, *op. cit.,* 2a: 174. Bonnet, 1958, *op. cit.,* 2: 3429.

Description. Carapace rather long and narrow, dark brown. Median light band spindle-shaped or with more or less parallel edges. Lateral bands yellow, wide and continuous, sometimes as wide as the dark bands. Near the edge of carapace a narrow dark band, often not clear, made up of dark spots and points (Fig. 3). Abdomen black with a yellowish lanceolate stripe on the anterior part followed by a row of whitish spots. They are often close to each other and make a single lanceolate band. Flanks whitish gray. Male darker than female. With carapace dark brown, bands usually

present though reduced or sometimes absent. Color of median and lateral bands reddish, the lateral ones sometimes broken. Abdomen black with gray or reddish pattern. Legs of female yellow with femora and tibiae annulated or blotched on upper sides. Metatarsi with one proximal and one distal dark ring. Sometimes, especially on the fourth metatarsi, there is also a median ring. Male with femora blotched on upper sides, darkened ventrally. Other segments uniformly yellow. Metatarsi of second pair ventrally with long hairs (Fig. 6). Male palpus (Figs. 4, 5) has femora blackish, patellae yellow with white hairs, tibiae and tarsi black. Epigynum as in Figure 7.

Remarks. The long-haired metatarsi of second pair of legs distinguish the male of *P. vittata* from all other species. Females have a characteristic epigynum and clearly differ from other *Pardosa*. *Pardosa bifasciata*, *P. schenkeli* and *P. nigriceps* have a body pattern much like that of *P. vittata*.

The characters used by Simon (1876, 1937) to separate *P. vittata* and *P. palitans* are, I believe, absolutely inadequate to distinguish the two species. I collected several specimens in different localities and many have characters of one or the other. Males generally have lateral bands on the carapace but very short spines on lower sides of anterior metatarsi. In females the width of lateral bands varies from specimen to specimen. On the other hand, Simon acknowledges that the characters distinctive of females are vague and variable (Simon, 1937, p. 1077, note). The genitalia of the two species are identical. It appears that *P. palitans* must be regarded as a synonym of *P. vittata*.

Ecology. This species is widespread but never very abundant. *Pardosa vittata* lives in moist places near streams, ponds, swamps and saltmarshes, on the plains as well as on the mountains as high as 1000 m.

Specimens examined from Italy. Emilia-Romagna. Modena: S. Anna Pelago, 1070 m, Appennino Tosco-Emiliano, 6.VII.1962; Forlì: Rimini (MSNF). *Toscana.* Lucca:

Massaciuccoli, 8.VI.1958; Pisa: S. Rossore, 7.VI.1958; Caprona, 5.VI.1960; Barbaricina, 6.VI.1960.

Specimens examined from outside Italy. Switzerland. Canton Ticino (Pavesi, MSNG). *Yugoslavia.* Dalmatia (MCZ). Istria: Pula, 28.VI.1962 (Levi, MCZ).

General distribution. France, Switzerland, Tyrol, Italy, Greece, Balkans to Caucasus.

Pardosa nigriceps (Thorell)
Figures 39–41

Lycosa nigriceps Thorell, 1856, Nova Act. reg. Soc. sci. Upsala, (3) 2 (1): 116. Female syntypes from Sweden.
Pardosa nigriceps,—Roewer, 1954, Katalog der Araneae, 2a: 168. Bonnet, 1958, Bibliographia Araneorum, 2: 3396.

Description. Carapace dark brown, rather long and narrow. Median and lateral bands wide. Median band reddish in the cephalic region, yellow in thoracic. Cephalic part of median band more or less oval in shape, divided from thoracic part by a thin transverse dark line and two spots. In the thoracic region the band gradually becomes narrower behind. The lateral bands yellow, extending to clypeus. They are separated from the edges of carapace by a narrow brown band. Sternum black with a wide yellow posteriorly-pointed stripe. Sternum almost black in male. Abdomen reddish brown, yellowish on sides and venter. Femora yellow with blotches above, other leg segments uniformly reddish. The male palpus (Figs. 39, 40) has a peculiar long terminal apophysis. Epigynum (Fig. 41) yellowish, the anterior part lightly sclerotized and rather variable.

Remarks. Both the male and female are clearly distinguished from all other Italian species of *Pardosa* by the shape of the genitalia. The carapace pattern of *P. nigriceps* is similar to that of *P. schenkeli*, *P. bifasciata* and *P. vittata*.

Ecology. According to Dahl and Dahl (1927) the species is characteristic of heaths. Simon (1937) says it is common also in swamps. Locket and Millidge (1951) indi-

cate that it is a common species in England on heaths and in open places having partly arboreal habitats. I have never found this species in Italy, although Bertkau (1890) records it from Liguria, and Caffi (1895) from Calabria. Mature specimens are found from May to July.

General distribution. All parts of Europe.

Pardosa lapponica (Thorell)
Figures 30–33

Lycosa lapponica Thorell, 1872, Remarks on Synonyms of European Spiders, p. 273. Male type from Karesuando, Lapland, Sweden.

Pardosa lapponica,—Roewer, 1954, Katalog der Araneae, 2a: 165. Bonnet, 1958, Bibliographia Araneorum, 2: 3380.

Description. Carapace brown. Median band consists of two round reddish spots in the cephalic region, divided by a dark line, a rhomboidal dark area behind and a reddish yellow band, slightly dilated at level of median furrow. The lateral light bands are yellow, continuous, extending to the clypeus. The lateral bands are separated from the edge of the carapace by a narrow dark band (Fig. 33). Lower spinnerets are dark in the female, black in the male. Upper spinnerets yellow in female, dark or black on dorsal side of male. The legs are reddish, femora slightly blotched. Male palpus (Figs. 30, 31) has a strong tooth behind tegular apophysis. Some white hairs dorsally on the distal part of the tibia. Epigynum as in Figure 32.

Remarks. *Pardosa lapponica* is closely related to *P. ferruginea* and *P. cavannae*. It is possible to distinguish these species by the very dark or black lower spinnerets. The male has a rather different tegular apophysis, and the shield and terminal apophysis are different. The females are distinguished by the different shape of the lips of the genital depression. *Pardosa lapponica* has a boreal-alpine distribution. It is closely related to many northern European species of *Pardosa* besides several North American ones, mainly *Pardosa concinna* (Thorell) and *P. glacialis* (Thorell). It is probably to *P. lapponica* that Calloni referred in his work "La fauna nivale" (1890) when he mentioned *P. glacialis* as one of the species of the Alpine fauna. (In this case Calloni would have distinguished *P. lapponica* from *P. cincta* Kulczynski.) Females of *P. lapponica* differ from those of *P. ferruginea* also by different shape of epigyna. The curvature of lips of the genital depression is different (compare Fig. 38). Drawings were made from Swedish and Tyrolean specimens.

Ecology. According to Calloni, this species occurs in the highest alpine regions, between 2000 and 2500 m in the eastern Alps. I examined one male specimen from Tyrol determined by Simon as *P. ferruginea* L. Koch (MNHN, No. 1386) and two males and two females from Abisko, Lapland, Sweden (Holm, MCZ).

Pardosa ferruginea (L. Koch)
Figures 36–38

Lycosa ferruginea L. Koch, 1870, Jahrb. k.k. Gelehr. Gesell. Krakau, 41: 46. Female holotype from Tatra Mountains, probably in the Berlin Museum.

Pardosa ferruginea,—Roewer, 1954, Katalog der Araneae, 2a: 162. Bonnet, 1958, Bibliographia Araneorum, 2: 3368.

Description. Carapace red-brown. Median light band reddish in the cephalic region and oval; yellowish and little dilated at level of median furrow in the thoracic region. Lateral bands very faint, narrow, distinct only posteriorly. Abdomen brown with a reddish yellow pattern covering most of the dorsum. Spinnerets brownish, about the same color as body. Legs of females reddish yellow, clearly annulated. Legs of males with femora reddish and annulated, other segments lighter, not annulated or with very pale annulations on posterior pairs.

Remarks. *Pardosa ferruginea* is closely related to *P. lapponica* and *P. cavannae*. The males are easily distinguishable from those of *P. lapponica* by the tegular and terminal apophysis and by the shield shape. Moreover, they do not have black spinnerets. Between *P. ferruginea* and *P. cavannae* the dif-

ferences are smaller, but the shape of the tegular apophysis is sufficient to distinguish them. Females of *P. ferruginea* differ from those of *P. lapponica* by the shape of the lips of the epigynum.

Ecology. *Pardosa ferruginea* lives in the Alps above 1000 m elevation in the conifer forests.

Specimens examined from Italy. Friuli-Venezia Giulia. Carnia (Di Caporiacco, MSNF).

Specimens examined from outside Italy. Switzerland. Val Tantermozza [Val Tavetsch] 1800 m (SMF). *Austria.* Engadina near Zernez, Bergwald, 1700 m (Grasshoff, SMF).

General distribution. France, Germany, Siberia, Italy, Balkans.

Pardosa cavannae Simon
Figures 34–35

Pardosa cavannae Simon, 1881, Boll. Soc. Ent. ital., 13: 21. Male holotype from top of Monte Amaro 2739 m, Majella Abruzzo, in the Muséum National d'Histoire Naturelle, Paris, examined.

Pardosa frigida,—Roewer, 1954, Katalog der Araneae, 2a: 163 (in part); Bonnet, 1958, Bibliographia Araneorum, 2: 3370 (in part). (Not *Pardosa frigida* Simon, 1876, Les Arachnides de France, Paris, 3: 353, pl. 13, fig. 15, ♀.)

Description. Carapace dark brown. Median light band absent. Lateral bands faint, narrow, of nearly the same color as carapace. Abdomen black with a reddish lanceolate stripe. Palpus as in Figures 34 and 35.

Remarks. The only mature specimen of *P. cavannae* is a male and differs from *P. ferruginea* by the shape of the tegular apophysis.

I consider *P. cavannae* different from *P. frigida* Simon, 1876, unlike Simon, who in 1937 synonymized *P. cavannae* with *P. frigida.* Simon described the male of *P. cavannae* and the female of *P. frigida,* and I do not think that the male of the first species matches the female of the other. Probably the female *P. cavannae* has an epigynum of the type of *P. ferruginea* and *P. lapponica,*

but the drawing of the epigynum of *P. frigida* has a quite different shape. Simon (1876) indicates that *P. frigida* is intermediate between *Pardosa* and the species group of *Lycosa cinerea* [the genus *Arctosa*]. *Pardosa cavannae* is a true *Pardosa. Pardosa cavannae* was described from the Appennines, while *P. frigida* is from the Alps (Faillefeu, Basse-Alpes, France).

Ecology. This species probably likes high altitudes. It was found on Mt. Amaro, 2739 m (Majella-Abruzzo) by G. Cavanna in August.

Pardosa paludicola (Clerck)
Figures 23–25

Araneus paludicola Clerck, 1757, Aranei Svecici, p. 94, pl. 4, fig. 7, ♂ ♀. Syntypes from Sweden lost.

Pardosa paludicola,—Roewer, 1954, Katalog der Araneae, 2a: 169. Bonnet, 1958, Bibliographia Araneorum, 2a: 3399.

Description. Carapace dark brown. Median and lateral bands reddish. Median band rather wide, slightly dilated in the cephalic and thoracic regions at level of median furrow, here also sometimes slightly branched. Lateral bands narrow and continuous around the carapace, serrated especially on the lower edges. Abdomen black with reddish pattern. Often the pattern covers all the dorsal side of the abdomen assuming a reddish color with only some black spots. Legs of female reddish brown. Legs of male reddish brown with femora blotched or annulated on upper side, other segments uniform. The genitalia are illustrated from French specimens.

Remarks. The male of *P. paludicola* is similar to that of *P. sordidata,* but the genitalia differ. The females of *P. paludicola* have a very characteristic epigynum, easily distinguishable from the nearest species: *P. sordidata* and *P. giebeli.*

Ecology. *Pardosa paludicola* lives on the plains as well as at moderate altitudes in the mountains. According to several authors it is common in meadows, vineyards, edges of woods, and near swampy places.

I have never collected this species, and among the spiders from Carnia, Romagna and Florence determined by Di Caporiacco there are no specimens of *P. paludicola*. I examined specimens from France (MNHN, MCZ). However, there are numerous literature references of this species occurring in Italy.

General distribution. Europe to Siberia, Turkestan (Turkmenistan), North Africa.

Pardosa sordidata (Thorell)
Figures 26–29

Lycosa sordidata Thorell, 1875, Tijdschr. Ent., 18: 105. Female holotype from Riesengebirge [Giant Mts. Poland-Czechoslovakia].

Pardosa sordidata,—Roewer, 1954, Katalog der Araneae, 2a: 172. Bonnet, 1958, Bibliographia Araneorum, 2: 3422.

Description. Carapace red-brown. Median band absent. Lateral light band only barely visible, more evident posteriorly, made up of two or three spots (Fig. 29). Abdomen blackish with brick red pattern. All colors are more marked on male, which has also very dark spinnerets. Femora of the female have two rings dorsally, uniformly dark ventrally. First and second femora darker ventrally. Other segments reddish without annulations. The male has the first femora black, slightly striped with yellow dorsally. Femora of second pair black along the proximal two-thirds of dorsal side and yellow-brown on the distal third. First and second femora are dark on ventral side. Third and fourth femora with two annulations dorsally, more or less darkened ventrally. Proximal half of first tibia almost black. First tarsus dark brown. Second tibia slightly darkened at base. Other segments yellow. The distinctive feature of the male palpus (Figs. 26, 27) is the bent lamina on the external side of shield. Epigynum as in Figure 28.

Remarks. *Pardosa sordidata* is closely related to *P. paludicola*. The genitalia of male and female are sufficient to distinguish the two species.

Ecology. This is a species of the mountain districts near 1500 m in coniferous forests and in *Pinus mugus* forests. *Pardosa sordidata* was found either near water courses or on meadows (Kulczynski, 1909: 686). I have examined 2 ♂ ♂ and 2 ♀ ♀ collected in Switzerland, Vaud: Caux, 1100–1500 m, 31.V.1958 (H. & L. Levi, MCZ). Mr. K. Thaler has recently found this species near Lake Garda (*in lett.*).

Pardosa lugubris (Walckenaer)
Figures 56–59

Araneae lugubris Walckenaer, 1802, Fauna Parisienne, 2: 239. Types from Paris vicinity, lost.

Pardosa lugubris,—Roewer, 1954, Katalog der Araneae, 2a: 166. Bonnet, 1958, Bibliographia Araneorum, 2: 3381.

Description. Females: carapace reddish brown. Light median band wide, with subparallel edges. Ocular trapezoid area covered with white hairs. Lateral bands indistinct, more evident posteriorly (Fig. 59). Male carapace dark brown. Median light band reddish in the cephalic region, yellowish in thoracic region. Ocular area and median band covered with white hairs. Lateral bands absent. Abdomen reddish brown with yellow-red pattern, darker with red pattern in males, and covered with white hairs as an extension of the median carapace band. Legs of females with annulations much clearer on femora and tibiae. Males have femora dark brown except distally, more or less annulated, other segments uniformly yellow. Male palpus (Figs. 56, 57) has brown segments covered with black hairs. Tip of long, narrow tarsus light. Septum of the epigynum characteristically anchor-shaped (Fig. 58).

Remarks. The males of the closely related *Pardosa lugubris* and *P. amentata* have similar palpi but the palpus of *P. amentata* (Figs. 60, 61) is wider than that of *P. lugubris*, and the carapace patterns differ. Females differ from *P. hortensis*, *P. proxima* and *P. cribrata* by carapace pattern and shape of epigynum.

Ecology. *Pardosa lugubris* is one of the most common Italian species. In woods, especially where there is little underbrush, numerous specimens are found running over

leaf litter. Specimens are mature from April through July and September. *Pardosa lugubris* lives in all parts of Italy in lowland to subalpine regions.

Specimens examined from Italy. Pie-monte. Casale Monferrato (Negri, MSNG). *Lombardia.* Pavia (MSNG). *Trentino.* Levico (Doria, MSNG). *Veneto.* Belluno (MSNF). *Friuli-Venezia Giulia.* Carnia (Di Caporiacco, MSNF). *Emilia-Romagna.* Modena: S. Anna Pelago, 1070 m, Appennino Tosco Emiliano. *Toscana.* Pisa: S. Rossore. *Campania.* Piano Acernese, 1163 m (Ruffo, MSNV). *Basilicata.* Matera: Policoro; Via Appia, km 491, 1000 m, between Potenza and Matera (Levi and Tongiorgi, MCZ).

Specimens examined from outside Italy. France. Manche: 2 km W of Quettehou (Lamore, MCZ); St. Vaast-la-Hougue (Lamore, MCZ). Seine et Marne: Woods of Fontainebleau (Levi, MCZ). Yonne: Champigny (Lamore, MCZ). Oise: near Chantilly (Levi, MCZ). Corsica (SMF). *Switzerland.* Vaud: Montreux, 400–1100 m (Levi, MCZ); Caux 1100–1500 m (Levi, MCZ). *England.* Surrey: Box Hill near Dorking (Levi, MCZ). *Germany.* Hessen: Eppenhain im Taunus (Levi, MCZ); Nieder Sachsen: Göttingen (Levi, MCZ). *Sweden.* Stockholm (Levi, MCZ). *Belgium.* Tervuren (Levi, MCZ). *Austria.* Tyrol: Seefeld, 1200 m, Karwendel Mts. (Levi, MCZ); Brixlegg (SMF). *Yugoslavia.* Istria: N slope of Mt. Ucka, 1100 m (Levi, MCZ). Slovenia: Bled 500–700 m (Levi, MCZ). Croatia: Plitvice (Levi, MCZ).

General distribution. Palearctic.

Pardosa amentata (Clerck)
Figures 60–63

Araneus amentatus Clerck, 1757, Aranei Svecici, p. 96, pl. 4, fig. 8, ♀ ♂. Syntypes from Sweden lost.

Pardosa amentata,—Roewer, 1954, Katalog der Araneae, 2a: 157. Bonnet, 1958, Bibliographia Araneorum, 2: 3351.

Description. Carapace brown. Median light band reddish in the cephalic region, yellow posteriorly; oval toward anterior, narrowed and again dilated at level of me-dian furrow, where it is slightly branched and more or less suddenly reduced at the posterior end. Lateral bands broken into three segments (Fig. 63). Male carapace brown or tawny. Usually median band evident only in thoracic region; lateral bands reduced or absent. Abdomen black with reddish pattern, often uniformly dark brown. Legs reddish yellow and clearly annulated in females. Males with femora blotched or striped on upper sides, more or less uniformly darkened on venter. Other segments uniform, only a little darkened or annulated on dorsal side.

Male palpus (Figs. 60, 61), segments very dark, almost black. Tibia and tarsus covered with very thick black hairs. Epigynum (Fig. 62) with a very characteristic semilunar area on the anterior part of genital depression.

Remarks. The male of *P. amentata* is separated from that of *P. lugubris* by the shape of tarsal segment of the palpus, which is much wider, and by the carapace pattern. The females of the two species can be separated by the shape of epigynum and body pattern.

Ecology. All authors indicate that *P. amentata* lives equally well on plains and in the mountains. I found this species to be common in alpine regions between 1000 m and 2000 m elevation, but never in flat country. It is found near water courses and in moist meadows. Mature specimens are found throughout the summer in the Alps.

Specimens examined from Italy. Pie-monte. Macugnaga, Val Anzasca: Alpe Cicerwald 1656 m; Alpe Burki, 1585 m; Val Quarazza, 1300, 1600 m; Monferrato: Lerma (Filippa, MSNG); Colle d'Olen, Alpi Pennine (Gnecco, MSNG); Lago Maggiore: Ascona (SMF). *Trentino.* Trento: Levico (Doria, MSNG). *Abruzzi-Molise.* Matese: Esule (MSNF). *Toscana.* Lucca: Capanne di Sillano, 1100 m, 4.VII.1965.

Specimens examined from outside Italy. France. Manche: St. Vaast-la-Hougue (Lamore, MCZ). *Switzerland.* Vaud: Montreux, 400–1100 m (Levi, MCZ); Caux, 1100–1500 m (Levi, MCZ). *Germany.* Nieder

Sachsen: Göttingen (Levi, MCZ). *Austria.* Tyrol: Seefeld, 1200 m, Karwendel Mts. (Levi, MCZ); Brixlegg (SMF); Pertisan (SMF); Salzburg: Fusch, 850 m, Hohe Tauern (Levi, MCZ); Garmig (SMF). *Yugoslavia.* Croatia: Plitvice (Levi, MCZ); Slovenia: Bled, 500–700 m, Alpi Giulie (Levi, MCZ). *Crete.* Topolia (Roewer, SMF).

General distribution. Europe to Siberia, Turkestan (Turkmenistan), North Africa.

Pardosa riparia (C. L. Koch)
Figures 42–45

Lycosa riparia C. L. Koch, 1833, Arachniden. *In* Panzer, Faunae Insectorum Germaniae initia, Heft 120, pl. 19. Male and female syntypes from Germany probably in the British Museum, London.

Pardosa kervillei,—Roewer, 1954, Katalog der Araneae, 2a: 164.

Pardosa riparia,—Bonnet, 1958, Bibliographia Araneorum, 2: 3417.

Description. Carapace brown or reddish brown, often dark brown in males. Median and lateral bands yellow or reddish yellow. Median band more or less spindle-shaped, sometimes slightly dilated anteriorly. Lateral bands separated from the edge of carapace by a dark band slightly narrower than the light ones (Fig. 44). Males sometimes have bands divided into three segments. Spinnerets dark brown. Legs yellow with reddish brown annulations. Tarsi yellow. Males have femora uniformly dark proximally and slightly annulated distally. Femora of first pair darker ventrally, fourth femora darkened along their length. Other segments uniformly yellow. Male palpus (Figs. 42, 43) with segments dark brown. Epigynum as in Figure 45.

Remarks. Both male and female are readily separated from *P. pullata, P. femoralis* and *P. prativaga* by the shape of the genital organs.

Ecology. This is a species of meadows, pastures and alpine regions between 1000 and 2000 m.[1]

Specimens examined from Italy. Valle d'Aosta. Gressoney la Trinité: Capanna S.

Anna, 2170 m. *Friuli-Venezia Giulia.* Carnia (Di Caporiacco, MSNF).

Specimens examined from outside Italy. Switzerland. Vaud: Caux 1100–1500 m (Levi, MCZ). *Austria.* Tyrol: Seefeld 1200 m, Karwendel Mts. (Levi, MCZ); Pertisan (SMF).

General distribution. Palearctic.

Pardosa pullata (Clerck)
Figures 49–51

Araneus pullatus Clerck, 1757, Aranei Svecici, p. 104. pl. 5, Fig. 7, ♀. Female holotype from Sweden lost.

Pardosa pullata,—Roewer, 1954, Katalog der Araneae, 2a: 171. Bonnet, 1958, Bibliographia Araneorum, 2: 3413.

Description. Carapace red-brown. Light median band regularly narrowed toward the posterior. Reddish in the cephalic region, yellow in thoracic region. Lateral band yellow, continuous, but often more or less broken into three segments; separated from margin of carapace by a darker band almost half as wide as the yellow one. Males generally darker, sometimes with lateral bands on carapace. Spinnerets dark. Leg annulations, if present, dorsally on femora only. On male, annulations limited to proximal half of femora. Other segments reddish in females, lighter in males, uniform. Tarsi yellow. In male palpus (Figs. 49, 50), ascending branch of tegular apophysis has a sharp tip. Seen from the side, the apex of the tegular apophysis is far from the edge of bulbus. Epigynum as in Figure 51.

Remarks. Males of *P. pullata* are closely related to those of *P. prativaga* and *P. femoralis,* but can be separated by the lack of annulations on legs. It is possible to distinguish them from *P. prativaga* by the different tegular apophysis, and from *P. femoralis* by the different shape of the

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[1] *Pardosa cursoria* (C. L. Koch) of Canestrini and Pavesi (1868, 1870), though regarded by Bonnet (1958) as *P. riparia,* would be much better referred to *P. blanda* (C. L. Koch). The reasons are given in the synonymy and in the observations about this species in P. Pavesi, 1873, Ragni del Canton Ticino, pp. 161–162.

lateral part of the tegulum. The epigynum is almost like that of *P. femoralis* but females can be separated by the different septum shape. The body pattern of *P. pullata*, as well as of *P. prativaga* and *P. femoralis* is like that of *P. riparia* (Fig. 44).

Ecology. This species prefers colder climates, and elevations to 2000 m. In England it is found with *P. prativaga* (Locket and Millidge, 1951) and it is regarded as one of the most common species of the genus. Simon (1937) says that it occurs throughout France. I have never found *P. pullata* in Italy, not even in places where *P. prativaga* is abundant, although there are numerous literature records of this species occurring in Italy.

Specimens examined from outside Italy. Denmark. Silkeberg (MCZ). *England.* Surrey: Box Hill, Dorking (Levi, MCZ). Hampshire: Stockbridge (Levi, MCZ). *Germany.* Hessen: Eppenhain im Taunus (Levi, MCZ). *Austria.* Salzburg: Fusch 850 m, Hohe Tauern (Levi, MCZ). *Switzerland.* Vaud: Caux 1100–1500 m (Levi, MCZ). *Spain.* Teruel, Sierra de Abrarracin (Kraus, SMF).

General distribution. All parts of Europe, Asia Minor to Turkestan (Turkmenistan).

Pardosa femoralis Simon
Figures 46–48

Pardosa femoralis Simon, 1876, Les Arachnides de France, Paris, 3: 345, pl. 13, figs. 13–14, ♀ ♂. Female, male syntypes from Pietra Cava, Maritime Alps in the Muséum National d'Histoire Naturelle. Paris, No. 18764, examined. Roewer, 1954, Katalog der Araneae, 2a: 162. Bonnet, 1958, Bibliographia Araneorum 2: 3367.

Lycosa montivaga Kulczynski, 1898, Razpr. spraw. wydzmat. przyred. Akad. Umiej., 36: 106, pl. 2, figs. 83, 84, ♀ ♂. Syntypes from Oberer Adlitzgraben, Semmering Pass, 180–1300 m, Austria, probably in the Budapest Museum.

Description. Carapace red-brown. Median light band yellowish clear only at level of median furrow. Lateral bands yellowish, slightly notched. Carapace of male almost black. Lateral bands, if present, divided into three portions. Femora dark with two or three annulations distinguishable. Other segments uniformly reddish yellow. Male palpus (Figs. 46, 47) with a pointed and sclerotized piece on the ectal part of tegulum. Epigynum (Fig. 48) with septum strongly dilated posteriorly and anterior edges dark and sclerotized.

Remarks. The male differs from that of *P. prativaga* by having the lateral piece of the tegulum larger and darker, by lacking white hairs on the palpus, and by lacking annulations on the legs. Possibly it can be separated from *P. pullata* by having the ascending branch of the tegular apophysis blunt at the end and reaching to the edge of the bulbus. The shape of the epigynum of *P. femoralis* is between that of *P. prativaga* and *P. pullata*. It is separated from the first by uniform coloration of the legs, from the second by having the septum of the epigynum shorter and wider posteriorly. Notwithstanding some discrepancies between the description of *P. montivaga* (Kulczynski) and the types of *P. femoralis*, I believe that it is possible to agree tentatively with the hypothesis of Dahl (1908), also adopted by Kratochvil (1935), about the identity of *P. montivaga* and *P. femoralis*. Roewer (1954, p. 165) considers *P. montivaga* to be a subspecies of *P. riparia* from an erroneous interpretation of work of Petrusewicz (1935). Petrusewicz indeed refers to *P. riparia* as *P. prativaga*.

Ecology. This is a mountain species.

Italian distribution. Pardosa femoralis has not been found within the political borders of Italy, but very close: e.g., Saint-Martin-Vesubie, Alpi Marittime. It must be considered as belonging to the Italian fauna. Of this species I examined, besides the syntypes, 3 ♀ and 1 ♂ from the Alps (MCZ). Drawings were made from French specimens.

General distribution. From Macedonia to the Pyrenees through the Alps.

Pardosa prativaga (L. Koch)
Figures 52–55

Lycosa prativaga L. Koch, 1870, Jahrb. k.k. Gelehr.

Gesell. Krakau, 41: 43. Female, male syntypes from Siebenbürgen, Merau, and Galacia,
probably in the Berlin Museum.

Pardosa fervida Simon, 1876, Les Arachnides de
France, 3: 336, pl. 13, fig. 17, ♀. Female
holotype from Corsica in the Muséum National
d'Histoire Naturelle, Paris, No. 1710, examined. Roewer, 1954, Katalog der Araneae, 2a:
162. Bonnet, 1958, Bibliographia Araneorum,
2: 3368. NEW SYNONYMY.

Pardosa prativaga,—Roewer, 1954, *op. cit.,* 2a: 170.
Bonnet, 1958. *op. cit.,* 2: 3408.

Description. Carapace red-brown. Median light band generally limited to the thoracic region only, yellow or reddish yellow.
Lateral bands separated from the edge of
carapace by a dark band almost as wide as
the light ones. Often the light bands are not
clear anteriorly, sometimes they are divided
into two or three segments. The male is
darker and the bands are often faint. Spinnerets brown. Legs of females yellow with
red-brown annulations, those of male with
very clear brown annulations. Male palpus
(Figs. 53, 54) has ascending branch of tegular aphophysis blunt at apex, which seen
from the side reaches the edge of the bulb.
Patella and tibia with white hairs on external side. Epigynum (Fig. 55) is variable.

Remarks. The males of *P. prativaga* can
be separated from those of *P. pullata* which
have the tegular apophysis, as seen from the
side, pointed and not reaching to the edge
of the bulbus. *Pardosa prativaga* differs
from *P. femoralis* by not having the ectal
corner of the tegulum sclerotized and
pointed. Females of *P. prativaga, P. pullata,*
and *P. femoralis* are easily separable by the
shape of epigynum. The carapace pattern is
like that of *P. riparia* (Fig. 44).

The holotype of *P. fervida* appears to be
a specimen of *P. prativaga.* On the basis of
body color it cannot even be referred to *P.
prativaga fulvipes* (Collett) (= *sphagnicola*
Dahl). Figure 52 shows the epigynum of
the holotype of *P. fervida.*

Ecology. Pardosa prativaga is common
and locally abundant. It is possible to find
it in damp fields and near swampy places,
especially on the plains. Near Pisa, speci

mens of both sexes are mature in May and
June.

Specimens examined from Italy. Piemonte. Torino: Pratiglione Ivrea, IV.1879
(MSNF). *Emilia-Romagna.* Forlì: Villagrande, 20.VII.1947 (Zangheri, CZ). *Toscana.* Pisa: S. Rossore, Spring 1958; Lucca:
Capanne di Sillano, 1100 m, 4.VII.1965.
Campania. Picentini Mts.: Piano Laceno
(Ruffo, MSNV). *Calabria.* Sila: Fago del
Soldato; Volpintesa; Lorica; Mt. Botte Donato; Silvana Mansio; Carmigliatello, 20–
26.VI.1960 (Ruffo, MSNV). Aspromonte:
Gambarie (Ruffo, MSNV).

*Specimens examined from outside Italy.
Finland.* Tvärminne, VIII.1959 (Papi).
Switzerland. Vaud: Montreux 400–1100 m
(Levi, MCZ).

General distribution. Europe to Siberia,
Kamchatka.

Pardosa luctinosa Simon
Figures 139–142

Pardosa luctinosa Simon, 1876, Les Arachnides de
France, 3: 347, pl. 13, figs. 24, 25, ♀ ♂. Male
and female syntypes from Corsica in the Muséum National d'Histoire Naturelle, Paris, No.
1709, examined. Roewer, 1954, Katalog der
Araneae, 2a: 165. Bonnet, 1958, Bibliographia
Araneorum, 2: 3381. Tongiorgi, 1964, Monit.
Zool. Ital., 72: 243–253.

Description. Carapace dark brown. Median light band reduced, generally more
evident and yellow in posterior region.
Lateral bands yellowish with serrated edges
and cut off at several points by dark lines
and spots (Fig. 141). Male darker than female. Median and lateral bands generally
faint or absent. Abdomen almost black,
anteriorly with a lanceolate yellowish stripe,
flanked by spots of the same color. The
lanceolate band is followed by a series of
four or five yellowish spots, often united
into a single band. On males only the gray
lanceolate stripe is generally visible. Legs of
females brown. One ring sometimes at the
distal ends of tibiae and metatarsi. Legs
of males have femora dark brown with a
light ventral spot on the apical third, or
sometimes a ring on the first leg. Patella

reddish yellow. Tibia and metatarsus reddish brown with a dark annulation on the proximal as well as on the distal end. Tarsi lighter. Male palpus (Figs. 139, 140), distal part of femur, patella, and tibia yellow on upper side, black ventrally. Tarsus dark. Tibia with white hairs on dorsal side. Epigynum as in Figure 142.

Remarks. Pardosa luctinosa is closely related to *P. italica.* The females have a similar epigynum but it is possible to separate them by color pattern. Lateral bands are continuous in *P. luctinosa*, while they are clearly broken in *P. italica; Pardosa luctinosa* lacks leg annulations; *P. italica* has legs clearly annulated. The males of the two species have a very different tegular apophysis. *Pardosa wagleri* differs from *P. luctinosa* by the genitalia. In the epigynum of the first species the septum is flat, while in *P. luctinosa* it has a posterior furrow. The tegular apophysis of *P. wagleri* is strongly hooked but that of *P. luctinosa* only a little.

Ecology. Pardosa luctinosa is halophilic and lives exclusively in saltmarshes or in places where the saline concentration of the ground and water is very high. *Salicornia* habitat is characteristic of this species, and here it is possible to find it together with *P. cribrata* (Tongiorgi, 1964).

Specimens examined from Italy. Veneto. 3 ♀ ♀ (Canestrini, IZUP). *Toscana.* Pisa: S. Rossore, 29.V.1958, 20.V.1962. *Puglia.* Bari: Barletta, 2.VI.1962.

General distribution. Corsica, Italy, Yugoslavia, Crete, Hungary, Russia, Turkestan, Siberia.

Pardosa italica n. sp.
Figures 135–138

Type. Male holotype and female paratype from Lago di S. Giuliano, Matera, Basilicata, 5.VI.1962 (P. Tongiorgi, H. W. Levi and L. R. Levi) in the Museo Civico di Storia Naturale, Genova.

Description. Carapace dark brown covered with gray pubescence. Median light band reddish yellow, generally limited to thoracic region. Two reddish spots behind the posterior lateral eyes. The median band is dilated at level of median furrow and faintly branched, then narrower posteriorly. Lateral light bands reddish yellow, clearly broken (Fig. 137). The two posterior spots sometimes joined. Male similar to female. Median band is often conspicuous, oval and dilated in the cephalic region. Clypeus yellow. Chelicera reddish yellow in the female, yellow in male, in both sexes darkened at the point. Sternum dark brown. Abdomen black covered with gray pubescence. Anterior lanceolate band reddish. Abdominal pattern consists of four brown spots, two on each side of the median band, and a series of yellow spots, the posterior ones fused. The abdomen of males has the median yellow spots flanked by two to three light spots. Generally there is one long spot in about the middle of the abdomen and another smaller spot more posteriorly. Females with legs reddish yellow, clearly annulated. Male with legs yellow. Femora annulated, tibiae with very pale annulations, metatarsi and tarsi uniform. Palpus (Figs. 135, 136) with segments yellow as are the first legs. Epigynum (Fig. 138) similar to that of *P. luctinosa.*

Remarks. Pardosa italica is closely related to *Pardosa luctinosa.* The females of the two species differ in carapace pattern. The median light band is indistinct and the lateral bands continuous in *P. luctinosa*, while in *P. italica* the median band is clear and the lateral ones broken. *Pardosa luctinosa* has the legs dark with annulations only on the femora, while *P. italica* has light and clearly annulated legs. The abdominal pattern is also different. The male is easily distinguished by the shape of the terminal and tegular apophysis; furthermore, the palpal articles are uniformly light. Both male and female are smaller than in *P. luctinosa. Pardosa italica* is easily distinguishable from *P. wagleri* by the genitalia.

Pardosa italica is the species to which the footnote in Tongiorgi, 1964, page 244, refers.

Ecology. Pardosa italica lives along the edges of rivers, streams and lakes at low elevations, another character that distinguishes

it from *P. luctinosa*, which lives exclusively in places of high salinity. Specimens are mature in June and July.

Specimens examined from Italy. Toscana. Pisa: Barbaricina, 19.VII.1963, 1 ♀. *Basilicata*. Matera: Lake of S. Giuliano, near the Via Appia antica (Levi, Tongiorgi, 5.VI.1962), 3 ♂ ♂, 3 ♀ ♀ (1 ♂, 1 ♀ paratype in MCZ). *Puglia*. Bari: Barletta, near the mouth of river Ofanto, 23.VI.1961, 1 ♂; 2. VI.1962, 2 ♀ ♀.

Pardosa wagleri (Hahn)
Figures 128–131

Lycosa wagleri Hahn, 1822, Monographie der Spinnen, 3 Heft, 10: 2.

Pardosa wagleri,—Roewer, 1954, Katalog der Araneae, 2a: 175. Bonnet, 1958, Bibliographia Araneorum, 2: 3430.

Description. Carapace brown, covered with gray pubescence. The gray pubescence causes living specimens to have an ash gray color. Median light band only in the thoracic region, indistinct, yellowish red. Lateral bands yellow, narrow and divided into three or four spots. Ocular area not darker than other parts of carapace, covered with gray hairs (Fig. 131). Male much darker than female. Median band almost absent, lateral bands reduced. The abdomen is gray-black, generally without pattern. Sometimes a yellow lanceolate stripe and some yellowish spots are present, but always indistinct. Often on the abdomen there are some spots and transverse lines made up of white pubescence. Legs yellow, blotched or annulated with brown; always very pale. Metatarsi uniform, especially those of fourth leg. Males have all metatarsi uniformly yellow.

Male palpus (Figs. 128, 129) with a characteristic tegular apophysis strongly bent. Palpal segments black, tip of tarsus light. Epigynum (Fig. 130) easily distinguishable by the slender septum. This may have a more or less long peduncle.

Remarks. The only species that can be confused with *P. wagleri* are *P. luctinosa* and *P. saturatior*. The males of *P. luctinosa* can be distinguished by the different shape of the tegular apophysis. The females differ in that the septum of the epigynum of *P. wagleri* is plain, while that of *P. luctinosa* is posteriorly hollow. The differences between *P. wagleri* and *P. saturatior* have been discussed under *P. saturatior*.

Ecology. Pardosa wagleri lives on the plain and up the mountains to middle altitudes. It likes stream beds and edges of rivers when these are pebbly or, less often, sandy. *Pardosa wagleri* can easily be seen running quickly on the water surface and sometimes also diving. The color of *P. wagleri* hides the animal among the stones. Contrary to the observations of Dahl (1908, p. 418), that *P. wagleri* lives only on the edges of water courses with rapid current, I found this species also on pebbly edges of streams that barely flow during summer. The species is mature from May to July.

Specimens examined from Italy. Piemonte. Alessandria: Casale Monferrato (Negri, MSNG); Lerma (Filippa, MSNG). *Liguria*. Albenga. *Toscana*. Lucca: Piano della Rocca; Barga; Livorno: Chioma Riv., 26.VI.1965. *Basilicata*. Potenza (Levi, Tongiorgi). *Puglia*. Bari: Barletta.

General distribution. European mountains from Spain to the Balkans.

Pardosa saturatior Simon
Figures 132–134

Pardosa wagleri var. *nigra* Dahl, 1908, Nova Acta Leopoldiana, 88: 380. Syntypes from Partnach 1100–1400 m [near Garmisch-Partenkirchen, Bavaria] probably at the Berlin Museum. Not *Pardosa nigra* (C. L. Koch).

Pardosa wagleri saturatior Simon, 1937, Les Arachnides de France, 6: 1067, 1124. New name for *P. wagleri nigra* Dahl.

Pardosa wagleri atra,—Roewer, 1954, Katalog der Araneae, 2a: 175 (in part). Not *Lycosa atra* Giebel, 1869.

Description. Carapace brown, very dark, covered with gray pubescence. Small median light band indistinct, reddish, limited to the thoracic region. Lateral bands yellowish, broken in three or four spots. Males have the carapace almost black and some reddish spots are scarcely perceptible along

the edges of carapace. Abdomen gray-black with only very faint pattern. The whole body color is rather dark. Legs of females reddish yellow, clearly annulated. Males have yellow legs with femora black (or annulated dorsally and black ventrally, except distally). Patellae and tibiae blotched dorsally, metatarsi and tarsi uniform. Generally, *P. saturatior* resembles *P. wagleri* but is larger and much more colorful.

The genital organs of both sexes are identical with those of *P. wagleri*, except in proportions. Differences in the illustrations of the two species may be due to individual variability and different rotation of palpus.

Remarks. Pardosa saturatior is separated from *P. wagleri* by being larger, darker, and living in a different habitat. *Pardosa wagleri* lives on the plains or at middle altitudes; *P. saturatior* lives in the alpine regions from 1500 m to the limits of glaciers and even higher. One sees *P. saturatior* running on moraines, on the debris that covers glaciers, and often on the ice itself.

P. wagleri and *P. saturatior* must be regarded as two different species. The two forms have similar genitalia, but are mainly separated by the size and differences in the ecology. They live at different altitudes, *P. wagleri* on plains and along the lower courses of rivers and of streams. The upper limit of this species must be located between 1000 to 1400 m, but most populations live between sea level and 300 to 400 m. *Pardosa saturatior* seems limited to altitudes above 1400 m, the optimal habitat being over 2000 m, near glaciers. The two do not come into contact or, if there is a zone of overlap it is in the area between about 1000 to 1400 m altitude; in this area the populations stay separate (Dahl, 1908, p. 418).

Further, the maturity periods of the two species differ. It is possible to collect mature *P. wagleri* males and females in June and July, but at the end of July the animals are rare and males have disappeared. In August we can find specimens of both sexes of *P. saturatior* and many females are carrying their egg sacs.

Specimens examined from Italy. Piemonte. Macugnaga: Belvedere Glacier, 1930 m, VIII.1962; Val Anzasca, 1500 m, VIII.1962; Val Quarazza, 1400 m, VII.1962. *Friuli-Venezia Giulia.* Carnia (Di Caporiacco, MSNF).

Specimens examined from outside Italy. Switzerland. Graubünden: Val del Diavel am Piz Quattervalls, 2000 m (Grasshoff, SMF). Graubünden National Park, Val Tantermozza [Val Tavetsch], 1800 m (Grasshoff, SMF).

General distribution. Alps.

Pardosa nebulosa (Thorell)
Figures 119–122

Tarentula nebulosa Thorell, 1872, Remarks on Synonyms of European Spiders, p. 330. Female holotype from Italy probably lost.

Pardosa nebulosa,—Roewer, 1954, Katalog der Araneae, 2a: 168. Bonnet, 1958, Bibliographia Araneorum, 2: 3394.

Description. Carapace brown. Median light band yellowish, strongly branched at level of thoracic furrow. Less clear and dilated as an oval spot behind the posterior row of eyes. Lateral bands yellow, distinct with irregular edges. Along edges of carapace dark spots are more or less evident (Fig. 121). The males sometimes have lateral bands clearly outlined in contrast to the interbranching of the median band by dark lines. Sternum dark brown, labium brown, maxillae yellow. Clypeus light brown. Legs yellow and clearly annulated in females. Generally, femora with three to four annulations not much extended on ventral side; one faint ring on patella; two on tibia, and one distal apical; three on metatarsi. The male has only the femora blotched on the upper side, other segments more or less uniform. Male palpus as in Figures 119, 120. Epigynum as in Figure 122.

Remarks. The only species of the Italian fauna that can be compared to *P. nebulosa* are *P. naevia* and *P. aenigmatica. Pardosa nebulosa,* one of the biggest Italian species

of *Pardosa*, was found in Italy by Canestrini according to Thorell. I examined some specimens from the Thorell collection preserved at the Natural History Museum of Stockholm, but among them did not find the female from Italy on which the description of the species, without doubt, was based. I saw the females from Dalmatia, also mentioned by Thorell (1872, p. 331), and males and females from Russia and Hungary. When the present study was already drafted I had the opportunity to examine also one Italian female specimen of *P. nebulosa* from the Canestrini collection (IZUP), and I have found that its morphology agrees perfectly with the other specimens of the same species that I had already examined. It is possible that it is the female described by Thorell.

General distribution. Italy, Hungary, Balkans to Caucasus. Thorell does not mention the place where the Italian specimens were collected.

Pardosa naevia (L. Koch)
Figure 126

Lycosa naevia L. Koch, 1875, Aegyptische und Abessinische Arachniden, p. 72, pl. 7, fig. 2, ♀ ♂. Female, male syntypes from Province Hamaszen, Ethiopia, in the Berlin Museum.

Pardosa naevia,—Roewer, 1954, Katalog der Araneae, 2a: 180. Bonnet, 1958, Bibliographia Araneorum, 2: 3394.

Description. Carapace dark brown. Light median band strongly branched in the thoracic region, expanded as an oval spot behind the posterior row of eyes. Lateral bands yellow, narrower than the dark ones. Related with the interrays of the branching median band, there are, on the lateral bands, two narrow darker lines, and near the edge of carapace, three black spots, the posterior of which is much more distinct (similar to the carapace of *P. nebulosa*, Fig. 121). Clypeus brown-black. Chelicerae reddish yellow. Maxillae yellow, labrum dark brown. Sternum black, a little lightened on sides. Abdomen black with yellow pattern, ventrally yellow. Legs reddish yellow. Femora, patellae and tibiae blotched

uniform. The male of this species has not been found yet in Sardinia.

Remarks. Identification of the specimens on hand with *P. naevia* is not certain. There are some differences in regard to the color patterns of the carapace between the description of *P. naevia* of Koch and my specimens, but the genitalia seem alike. *Pardosa nebulosa* and *P. naevia* have a similar carapace pattern but different genitalia. The females of *Pardosa naevia* are easily separated from those of *P. aenigmatica* by the carapace pattern.

The species heretofore has been known only from Ethiopia. Since our knowledge of the lycosids of North Africa is very scarce, it can not be excluded that the distribution of *P. naevia* reaches the Mediterranean basin.

Specimens examined from Italy. Sardegna. 1 ♀ (SMF); Cagliari: Guspini (Oristano Campidano), May, 1924, 2 ♀ ♀ (Ferruglio, MSNF).

General distribution: Ethiopia, Sardinia.

Pardosa aenigmatica n. sp.
Figure 127

Type. Female holotype from Esule, mountains of Matese, Abruzzi Molise, 16. VII.1874. (G. Cavanna) in the Museo di Storia Naturale, Firenze.

Note. One female paratype in Museo Civico di Storia Naturale, Genova and one female paratype in Museum of Comparative Zoology, Cambridge.

Description. Carapace red-brown. Median light band spindle-shaped, not particularly prominent. Lateral bands broken into three segments, hardly lighter than the carapace. Abdomen black with a reddish pattern. Legs reddish brown. Femora with three brown annulations more or less darkened; other segments blotched or darkened on the ventral sides. Carapace length 3 mm, width 2.2 mm. Total body length 7.0 mm. Length of first femur 2 mm, patella–tibia 2.5 mm, metatarsus 1.5 mm, total length of first leg 7.2 mm. Fourth femur 2.6 mm, patella–tibia 3.5 mm, metatarsus 3.2

and annulated with brown; other segments mm. Total length of fourth leg 11.1 mm. Epigynum as in Figure 127.

Remarks. Pardosa aenigmatica is related to *P. naevia*, judging by the shape of the epigynum, but has a different body color pattern. The specimens do not fit any other species described for Italy or southern Europe. Only the description of *P. frigida* is close, but the body size and shape of the epigynum of this species are different. Unfortunately, the type of *P. frigida* is lost. I do not think that the females of *P. aenigmatica* belong with the male of *P. cavannae* (see *P. cavannae* for further discussion). Some North African species have epigyna closely resembling that of *P. aenigmatica* but none fits exactly. It will be necessary to study the male to learn the relationship of *P. aenigmatica*.

Italian distribution. Abruzzi-Molise. Mountains of Matese.

Pardosa cribrata Simon
Figures 148, 149, 152, 153

Pardosa cribrata Simon, 1876, Les Arachnides de France, 3: 342. Female, male syntypes from the Gulfe du Lion, southern France, in the Muséum National d'Histoire Naturelle, Paris. Roewer, 1954, Katalog der Araneae, 2a: 161. Bonnet, 1958, Bibliographia Araneorum 2: 3365.

Description. Carapace dark brown. Light median band yellow, spindle-shaped, sometimes a little extended beyond the line of the posterior eyes. Lateral bands yellow but not very evident, being covered with little dark spots and black hairs. They are continuous and are kept apart from the edge of the carapace by a well-marked black line (Fig. 148). Carapace of male darker and lateral bands less distinct. Abdomen blackish speckled with yellow. The whole body, particularly the abdomen of *P. cribrata*, has a greenish cast that is more evident on animals that have been preserved in alcohol for a short time. Abdominal pattern yellow. The four or five spots following the anterior lanceolate band are sometimes more or less fused. Legs on females reddish

yellow, strongly blotched and annulated dark; seldom yellow with pale annulations. Legs of males yellow; femora of first pair black, those of the other legs blotched on upper sides and ventrally darkened. Other segments dusky. Male palpus as in Figures 152, 153. Epigynum as in Figure 149.

Remarks. Pardosa cribrata can be separated from *P. hortensis* and *P. proxima*, with which it is very often collected, by the following characters: the male is separated by carapace pattern from males of *P. hortensis*. The shape of the terminal and tegular apophysis is sufficient to separate the males of *P. cribrata* and *P. proxima*. Females of *P. cribrata* are easily separated from those of the other two species by the carapace pattern. *Pardosa hortensis* has the median band clearly dilated in front and at the median region; *P. proxima* and *P. cribrata* have a spindle-shaped median band and the lateral bands broken. Since it resembles *P. hortensis* and *P. proxima* it must often have been confused with those two species; otherwise we could not explain the few records of the Italian collectors.

Note. Near Nuova Siri, Calabria, on the sandy edges of a stream near the sea, Prof. F. Papi collected several male and female specimens of a *Pardosa* that I tentatively placed in *P. cribrata catalonica* Simon (Simon, 1937, p. 1075, female holotype from Menton, Maritime Alps, in MNHN). The specimens have genitalia like those of *P. cribrata* but the size is much smaller and color lighter. The sternum in both sexes is yellow, sometimes in females a little darker on sides, and in males brown with a large median yellow spot. The carapace is brown in both sexes but much lighter than in typical specimens. The median band is wider and a little dilated anteriorly in several specimens. The lateral bands are more clear cut. The abdomen of females is almost yellow, darker in males, but rather light posteriorly. Legs of females are yellow with very pale annulations or without rings.

It is with some doubt that I regard these specimens as belonging to the subspecies

P. cribrata catalonica. Not very far away, near Metaponto, I collected typical specimens of *P. cribrata cribrata*, and I do not see any reason to consider the two localities or the spider populations ecologically or geographically divided. On the other hand, specimens of smaller size and lighter color of other species were collected on the slopes of Monte Pollino and in Sila (see *P. monticola*). [The drawings of *P. cribrata*, that of the male in particular, made by Roewer (1958, p. 50, fig. 10 a–c) are rather different and do not fit the European specimens.]

Ecology. Pardosa cribrata is a common species. The habitat of this species is dry places near rivers, streams, ponds and marshes. It is possible to find it also on fields either in the low country or in mountains. The most typical habitat is edges of salt marshes where it is found with *P. luctinosa* which it resembles in carapace pattern and color. The species is mature in April and July.

Specimens examined from Italy. Piemonte. Alessandria: Casale Monferrato (Negri, MSNG). *Emilia-Romagna.* Ravenna: S. Alberto, 12.V.1947 (Zangheri, CZ). *Toscana.* Pisa: 6.IV.1960; S. Rossore, 27.V.1958, 7.VI.1958, 20.V.1952, 17.V.1963; Barbaricina, 19.VII.1963. Caprona. Lucca: Massaciuccoli, 7.VII.1963. Levigliani, Alpi Apuane, 660 m, 4.VI.1960. Livorno: Stagno, 22.VII.1963. Siena: Lugnano (MSNF). *Puglie.* Bari: Barletta, mouth of river Ofanto, 2.VI.1962; Canne, 23.VI.1961; Taranto: edges of river Lato, June 1962. *Basilicata.* Matera: Metaponto, 14.VI.1961; Lake of S. Guiliano Matera, 5.VI.1962. *Sardegna.* 1 ♀ (SMF).

General distribution. France, Spain, Italy.

Pardosa proxima (C. L. Koch)
Figures 146–147, 156–157

Lycosa proxima C. L. Koch, 1848, Die Arachniden, 15: 53, figs. 1453, 1454, ♂ ♀. Female, male syntypes from Greece, probably in the British Museum, London.

Pardosa proxima,—Roewer, 1954, Katalog der Araneae, 2a: 171. Bonnet, 1958, Bibliographia Araneorum, 2: 3410.

Description. Carapace reddish brown. Median and lateral bands yellow. The median band spindle-shaped, the lateral ones clearly broken into three or, more rarely, four spots (Fig. 146). Males only a little darker than females with bands equally distinct. Sternum reddish brown. Abdomen brown with reddish yellow or reddish pattern, often not very clear. Legs of females reddish yellow with brown annulations. The males have femora of first pair black or darkened, femora of other pairs annulated. Other segments yellow suffused with dark. Male palpus (Figs. 156, 157) has all segments reddish brown. Epigynum as in Figure 147.

Remarks. Pardosa proxima differs from *P. hortensis* by carapace pattern. Males are easily separated from those of *P. hortensis* because they have all palpal segments redbrown while in *P. hortensis*, femur and patella are yellow and the other two segments black. Both males and females closely resemble *P. cribrata.* The continuous lateral bands and the greenish color of body separate *P. cribrata* from *P. proxima.*

The individual variability of *P. proxima* is great even within the same population. For example, I have collected on the edges of Fiume Centa (Albenga, 30.VI.1958) a female specimen that has an epigynum identical to that of *P. proxima*, but the median band of the carapace is anteriorly dilated and the lateral bands are continuous and very wide. All legs are yellow without annulations. Some authors have attempted to distinguish also, in Italy, the subspecies *P. proxima poetica* Simon and *P. proxima tenuipes* (L. Koch) from the typical form *P. proxima proxima* (C. L. Koch). Since the two subspecies in question do not display a geographical separation in the Italian peninsula, and in fact they have been found together, I believe that they represent different aspects of variability of *P. proxima.* Nearly all the specimens I have examined belong to the typical form. The femora of

the first pair of legs of males are generally very dark and sometimes even black.

Ecology. This species has a widespread distribution. It lives in all parts of Italy, mostly on meadows, along the exposed stream beds, on the edges of ponds, lakes, and swampy places. It is also common in fields together with *P. hortensis.* It lives at low as well as middle altitudes. Specimens mature in spring and summer.

Specimens examined from Italy. Piemonte. Alessandria: Casale Monferrato (Negri, MSNG). *Liguria.* Genova (MSNG); La Spezia (Mazza); Albenga. *Emilia-Romagna.* Forlì: Ladino, Carpena, Colmano, Cappuccinini (Zangheri, CZ). *Toscana.* Firenze: Piccioli (Cavanna, MSNF), S. Gervasio (Di Caporiacco, MSNF). Arezzo: Monterchi (Di Caporiacco, MSNF). Livorno: Stagno. Lucca: Levigliani, Alpi Apuane, 600 m; Pania della Croce, Alpi Apuane, 1170 m; Massaciuccoli (some specimens with continuous lateral bands). Pisa: S. Rossore; Barbaricina; Caprona; S. Giuliano. Island of Giglio (Doria, MSNG); Island of Capraia (D'Albertis, MSNG); Island of Elba: Poggio (Kraus, SMF). *Sicilia.* Siracusa: Mt. Lauro, Iblei Mts. (Alicata); Brucoli (Alicata). Palermo: Bisacquino, Mt. Gennardo, 800 m, Mt. Triona (Alicata). Messina: Portella Femmina Morta, Nebrodi Mts. (Alicata).

Specimens examined from outside Italy. Yugoslavia. Istria: near Pula (Levi, MCZ). Examined also specimens from Corsica, Germany, Austria, Macedonia, Albania, Crete (SMF).

General distribution. Great Britain, central and southern Europe, Balkans to Mesopotamia, North Africa, Canary Islands, Azores.

Pardosa hortensis (Thorell)
Figures 150–151, 154–155

Lycosa hortensis Thorell, 1872, Remarks on Synonyms of European Spiders, p. 299. Female and male syntypes from Pyrmont (Waldeck) and Nürnberg, Germany.

Pardosa hortensis,—Roewer, 1954, Katalog der Araneae, 2a: 163. Bonnet, 1958, Bibliographia Araneorum, 2: 3374.

Description. Carapace reddish brown. Median light band expanded in cephalic region and in thoracic region at level of median furrow. Lateral bands reddish yellow, broken (Fig. 150). Abdomen brown with yellow tawny pattern. The male generally has the median band evident only on the thoracic region and lateral bands indistinct. The legs clearly annulated on females. The males have all femora and segments of third and fourth legs annulated; patellae, tibiae, tarsi and metatarsi of first and second legs yellow and uniform. Male palpus with yellowish femur and patella contrasting strongly against the black tibia and tarsus. The little terminal apophysis is located under the laminar process of shield (Figs. 154, 155). Epigynum (Fig. 151) has the septum variable. It can be shaped simply as an upside-down T or the septum may be dilated in the middle, constricted between the dilation and the transverse portion.

Remarks. Both sexes of *P. hortensis* differ from *P. proxima* by carapace pattern. The median band is dilated in *P. hortensis* but spindle-shaped in *P. proxima.* The species is separated from *P. cribrata* by the shape of the median and lateral bands, which are continuous. A careful examination is necessary to distinguish the females of *P. hortensis* from those of *P. strigillata* and *P. pseudostrigillata.* Females are easily separated from those of *P. lugubris* by body pattern.

Ecology. Together with *P. proxima*, *P. hortensis* is the common Italian species. *Pardosa hortensis* lives in dry places as well as in moist ones. It is particularly abundant on meadows and fields. It lives from low to middle altitudes. Mature specimens are found in the spring, females also in summer and fall through October.

Specimens examined from Italy. Piemonte. Alessandria: Lerma (Filippa, MSNG). *Friuli-Venezia Giulia.* Carnia (Di Caporiacco, MSNF). *Veneto* (Canestrini,

IZUP). *Emilia-Romagna*. Forlì: Premilcuore, Cappuccinini (Zangheri, CZ); Ravenna: Pineta S. Vitale (Zangheri, CZ); Modena: S. Anna Pelago, 1070 m. *Toscana*. Firenze: Piccioli, Carmignano; Lastra a Signa, Mt. Fiesole (Di Caporiacco, MSNF). S. Marcello Pistoiese: Mt. Teso, 1500 m (Cavanna, MSNF). Arezzo: Passo of Consuma, 1023 m (MSNF). Livorno: Gabbro. Lucca: Bagni di Lucca, Levigliani, 600 m, Alpi Apuane. Pisa: S. Rossore; Barbaricina, Montemagno, Caprona, S. Giuliano. *Campania*. Ravello (Levi, MCZ). Lattari Mts., 800 m, between Gragnano and Agerola, peninsula Sorrentina (Levi, MCZ). *Basilicata*. Stream Percopo, near river Bradano; Km 491 Via Appia; between Potenza and Matera; Potenza, 800 m (Levi, Tongiorgi, MCZ). *Puglia*. Bari: Gioia del Colle. *Calabria*. Sila: Lake Cecita (Papi).

Specimens examined from outside Italy. *Yugoslavia*. Istria: N slope of Mt. Ucka, 1100 m (Levi, MCZ). *Slovenia*: Bled, 500–700 m, Alpi Giulie (Levi, MCZ).

General distribution. Great Britain, central, eastern and southern Europe to Caucasus, North Africa, Japan.

Pardosa strigillata Simon
Figures 143–144, 158–159

?*Lycosa atomaria* C. L. Koch, 1848, Die Arachniden, 15: 31, fig. 1437, ♀. Female holotype from Nauplia, Greece.

Lycosa strenua Thorell, 1872, Remarks on Synonyms of European Spiders, p. 302. Female syntypes from Italy. (Not *L. strenua* Nicolet, 1849; not *L. strenua* Rainbow, 1920.)

Pardosa strigillata Simon, 1876, Les Arachnides de France, 3: 338, pl. 12, fig. 6, pl. 13, figs. 9, 10, ♀ ♂. Female, male syntypes from Corsica in the Muséum National d'Histoire Naturelle, Paris. Roewer, 1954, Katalog der Araneae, 2a: 173. Bonnet, 1958, Bibliographia Araneorum 2: 3424.

Pardosa subita Simon, 1876, *op. cit.*, 3: 356. (New name for *L. strenua* Thorell.) (Not *Lycosa subita*,—Kulczynski, 1887.)

Pardosa atomaria,—Roewer, 1954, *op. cit.*, 2a: 159. Bonnet, 1958, *op. cit.*, 2: 3358.

Description. Carapace dark reddish brown. Light median band yellow, dilated anteriorly and at level of thoracic furrow, where it is clearly branched. Lateral bands yellow, broken, with irregular edges (Fig. 143). At times the lateral bands are continuous but serrated. Male as female, but darker. Sternum black. Abdomen generally black with yellow pattern. Anterior lanceolate band reddish yellow. The yellow pattern takes up most of dorsal side of abdomen. It is not difficult to find specimens with the abdomen very light; the dark parts are then reduced to small loose spots. Legs reddish yellow, clearly annulated on the female, less on the male. Palpus (Figs. 158, 159) with femora black, and distal end and lateral sides yellow. Patellae yellow; tibiae and tarsi black. Epigynum as in Figure 144.

Remarks. *Pardosa strigillata* is closely related to *P. pseudostrigillata*. The males of the two species differ mainly by the shape of the tegular apophysis (compare Figs. 160, 161). In contrast, females are very difficult to separate. There are, indeed, some small differences in the shape of the epigynum and in spination of the first legs, that may be used successfully to separate the two species. In the color of carapace and structure of genital organs, *P. strigillata* is very like *P. hortensis*. A careful inspection of morphological characters is, therefore, necessary. As the synonymy of *Pardosa strigillata* is rather confused, I will summarize it briefly.

In 1872 Thorell described, without providing any drawing, *Lycosa strenua*. The name *strenua* could not be maintained, because it was preoccupied by the *Lycosa strenua* Nicolet, and therefore Simon (1876, p. 356) renamed it *P. subita*. At the same time, Simon (1876, p. 338) described *P. strigillata*, the description of which fits rather well the original description that Thorell had given of *L. strenua*. In fact, Simon in 1937 considered *P. subita* as a synonym of *P. strigillata*. The drawings of *P. strigillata* published by Simon (1876, 1937), though not very clear, permit the identification of the species.

I was able to examine many specimens of both sexes of *P. strigillata* collected in Sardinia and Corsica (Kraus det., SMF). I examined also six females and one male collected at La Spezia and Canton Ticino (Collection Canestrini, IZUP). The specimens of the Canestrini collection are labelled as *Lycosa strenua* Thorell and it is very likely that the original description of *P. strenua* by Thorell himself was based on the two females of this group (Thorell, 1872, p. 303).

There is another species very closely related to *P. strigillata*, namely *Pardosa atomaria* (C. L. Koch) (C. L. Koch, 1848, fig. 1437). The original description and drawing are unfortunately too poor and therefore inadequate to identify the species, and there is no other description or illustration of *P. atomaria* based on the original material which, as far as I know, is lost.

The drawing of the epigynum of a female of *P. atomaria* given by Kulczynski (1908, pl. 2, fig. 23), though well done, could be referred to *P. strigillata* and *P. pseudostrigillata* as well. Kulczynski himself ascribes his specimen only tentatively to *P. atomaria*. The figures of the palpus and the epigynum given by Giltay (1932) are uselessly schematic. Therefore, I consider *P. atomaria* (C. L. Koch) a doubtful species. Because the type as well as the other described specimens of *P. atomaria* come from the Balkans and Asia Minor where *P. strigillata* is rather common, and because, on the basis of the drawings of C. L. Koch, Kulczynski and Giltay, it is impossible to distinguish the two species, I would be inclined to consider *atomaria* as a synonym for *strigillata*.

Ecology. Pardosa strigillata lives on sandy places especially along edges of streams (Simon, 1937) as high as 400–500 m. Denis (1952) records the capture of one female at 2120 m on the massif du Carlit (east Pyrenees). Mature specimens of both sexes have been collected in April, mature females also in September. I could not examine any specimens of *P. s. ligurica* Simon.

Italian distribution. Pardosa strigillata seems to replace *P. hortensis* in Sardinia. It is one of the more frequent species on the island, while *P. hortensis* is almost unknown there. The only two records of *P. hortensis* in Sardinia are those of Magretti (1880) and Garnari (1902), and they could easily have mistaken it for *P. strigillata*.

As for the other Italian records, among the spiders of Carnia (Di Caporiacco, 1922, 1927), and Romagna (Di Caporiacco, 1926, 1938, 1949), and Umbria (Di Caporiacco, 1950), I have not found any specimen of *P. strigillata*. All specimens identified as *P. strigillata* by Di Caporiacco were either juvenile specimens (especially of *P. hortensis*) or misidentified. I could not check other records. Probably it would be much better to assign the records in the province of Florence to *P. pseudostrigillata* (Di Caporiacco, 1923, 1936).

Specimens examined from Italy. Liguria. La Spezia (Canestrini, 1873, IZUP). *Sardegna.* S. Vito, Sarrabus, IV.1872 (Gestro, MSNG). Sassari: Ozieri, 320 m, Lagadozo, 21.IV.1955 (Kahmann leg. Kraus det., SMF).

Specimens examined from outside Italy. Besides the specimens of *P. strigillata* of Italy and Sardinia, I saw several females from Crete, Skyros and Vityna (Greece), and from Montenegro. (Unfortunately, I have not found any male among them so the identification remains doubtful.) These specimens, by the characters indicated above, are *P. strigillata*.

France. Corsica: Biguglia, 28.IV.1952; Asco Tal 17.IX.1953; Stream Prunelli 17.IV.1955; Lucciana, 21.IV.1954; Corte, 15.IV.1952 (leg. Kahmann, det. Kraus 1955, SMF). *Yugoslavia.* Montenegro: Radakovic, 17.VIII.1959; Petrovac, 16.VIII.1959 (Papi). *Greece.* Archadia; Peloponneso: Vityna VII.1926 (Roewer, SMF); Tripolitza (Roewer, SMF); Pikermi (D'Albertis, MSNG). Sporadi, Isl. Skyros, 22.III.1958 (Schelkept, SMF). *Crete,* VI.1926 (Roewer, SMF).

General distribution. Southern Europe from Portugal, France to the Balkans.

Pardosa pseudostrigillata n. sp.
Figures 145, 160–161
Lycosa subita,—Kulczynski, 1887. Rozpr. Spraw.

Wydz. Mat. Przvyred. Akad. Umiej., 16: 254, pl. 5, figs. 4–5, ♀ ♂. (Not *P. subita* Simon, 1876.)

?*Lycosa maculata* Rosca, 1939, Zool. Anz., 125(3, 4): 95, figs. 6–9 ♂ ♀. Male and female syntypes from Dobrogea, Roumania, destroyed. (Fuhn, *in litt.* to Dr. H. W. Levi.)

Type. Male holotype from Cerreto, Tosco-Emiliano Appennins, Italy, in the Museo di Storia Naturale, Genova.

Description. Pardosa pseudostrigillata, as far as we know, has a body pattern similar to that of *P. strigillata*. The differences between the two species are here described. The genitalia are illustrated by Figures 145, 160, 161.

Remarks. Pardosa maculata (Rosca) is very close to *P. pseudostrigillata*. On the drawing of Rosca's species it is possible to observe a laminar process of the shield on the male bulbus. Besides *P. hortensis*, which has a similar process but, according to Rosca, different structure of the palpus, I know of only one other similar species, *P. pseudostrigillata*. The form I give here as *Pardosa pseudostrigillata* is identical to the one that Kulczynski (1887) described under the name of *P. strenua* [= *P. strigillata*].

Actually, though it was not pointed out in the text of Kulczynski, the drawings (at least that of the male palpus) of this author reveal substantial differences between this species and *P. strigillata*. The tegular apophysis of the male palpus is undoubtedly different. The description of the female does not allow differentiation of the two species.

The males I was able to study (two collected at Cerreto[1] and one in province of Forlì) are certainly identical to that represented by Kulczynski. On a lot of females collected at Villa Mercatale, near Florence,

I was able to find some characters that permit differentiating them from typical *P. strigillata*. They are:

1) On all specimens of *P. strigillata* that I examined, the basal spines of anterior metatarsi hardly reach the base of the median ones (cf. Simon, 1937, p. 1080). On the specimens of *P. pseudostrigillata* the basal spines are longer, overlapping the middle of the median ones.

2) Ventral to the first tibia of *P. strigillata* there are two pairs of spines. A third pair is placed more apically and shifted sideways. The spines are rather thin and short. In *P. pseudostrigillata* there are three pairs of spines on the ventral sides of the first tibia, the third pair being in a line with the other two pairs. Besides, spines are longer and stronger. These characters can be sometimes variable, particularly the position of the third pair of spines.

3) In all the specimens of *P. pseudostrigillata* that I have examined, a dark sclerotized process that protrudes from the anterior corner of each pocket of the epigynal septum is present (Fig. 145). This process is not distinctly visible in *P. strigillata* and I do not know whether this character can have a taxonomic value.

On this basis I have tentatively ascribed these females to *P. pseudostrigillata*. Only after this paper was submitted have I been able to study one male and one female of *P. pseudostrigillata* kindly sent to me by Mr. K. Thaler of Innsbruck. They were collected near Limone, Garda Lake, 31.V.1963, in a talus field with scanty vegetation near a stream at 300 m elevation. I can now confirm that the above-mentioned females match the male of *P. pseudostrigillata*.

Specimens examined from Italy. Emilia-Romagna. Forlì: Lardiano, 4.XI.1923, 1 ♂, 3 ♀ ♀ juv. (Zangheri, CZ). Reggio Emilia: Cerreto, 1 ♂ (MSNG). *Toscana.* Firenze: Vinci, Villa Mercatale, 60 m, 19.VI.1921 (Di Caporiacco, MSNF) (determined by Di Caporiacco as *P. strigillata* and *P. amentata*).

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[1] *Note.* On the label in the vial the name of the locality is only shown as Cerreto. The specimens have been probably collected at Passo del Cerreto. (Reggio Emilia, Appennino Tosco Emiliano), but in Italy there are many other localities so named. Some are in Tuscany and in Florence province.

Pardosa morosa (L. Koch)
Figures 64–66

Lycosa morosa L. Koch, 1870, Jahrb. k.k. Gelehr. Gesell. Krakau, 41: 47. Female syntypes from several localities in the Tatra mountains and Bohemia, probably in the Berlin Museum.

Pardosops morosa,—Roewer, 1954, Katalog der Araneae, 2a: 197.

Pardosa morosa,—Bonnet, 1958, Bibliographia Araneorum, 2: 3393.

Description. General color of body very dark. Carapace wide and very dark brown. Median light band reddish yellow. It is generally clear at level of median furrow where it appears as a branched spot. Sometimes on the cephalic region there is a lighter area or yellowish spots. The lateral bands are broken into three or more rather narrow spots. The male is darker. Abdomen dark brown with indistinct red pattern. Legs red-brown with dark annulations. Male legs more or less uniformly darkened. Male palpus as in Figures 64, 65. Epigynum as in Figure 66.

Remarks. *Pardosa morosa* is closely related to *P. strigillata* and *P. pseudostrigillata*. The male is separated from others by the different shape of the process of shield. This process is rather blunt and short in *P. morosa* but flattened and slender in *P. strigillata* and *P. pseudostrigillata*. Females of this species are separated by color pattern.

Ecology. According to Simon, Dahl, and de Lessert the characteristic habitat of *P. morosa* is the same as that of *P. wagleri*, the edges of lakes, rivers and streams made up of pebbles, stones or, at least, rough sand. I have never found *P. morosa* with *P. wagleri* either on the plains or in the mountains. According to de Lessert (1910), this species is common on the lake of Geneva and along the banks of the Rhone. It is likely that *P. morosa* will be found in Italy in zones of middle altitude.

Italian distribution. Among spiders from Carnia and Romagna identified by Di Caporiacco are specimens classified as *P. morosa* but either these are juveniles or the identification is wrong. I examined specimens from France and Galicia (MCZ) and

from Lausanne (det. by Pavesi as *P. paludicola*, MSNG). Other records are by Di Caporiacco (1951a), Bertkau (1890) and Jackson (1926).

General distribution. France, Central Europe to Poland, Italy to Balkans.

SPECIES OF DOUBTFUL OCCURRENCE IN ITALY, AND QUESTIONABLE SPECIES

Pardosa arenicola (O. P.-Cambridge)
Figures 75–76

Lycosa arenicola O.P.-Cambridge, 1875, Ann. Mag. Nat. Hist., (4)16: 253, pl. 8, fig. 9a, b, ♀ ♂. Male and female syntypes from Island of Portland, Chesil Beach, England, in the University Museum, Oxford.

This species was twice recorded for Italy by Di Caporiacco (1940, 1950). It is a northern European species and the females can be separated only with difficulty from those of other species of *P. monticola* group. The identification of specimens collected on Cima Galbana, 1583 m (Lessini Mts., Verona) [This collection was lost during the last war], is probably wrong because it is far from the typical habitat. The female collected on a sandbank of S. Giuliano (Laguna di Venezia) could be this species but the identification carried out on only one female is questionable. I have never been able to collect *P. arenicola* nor could I check the identity of Di Caporiacco's specimens. Therefore I question the presence of this species in Italy. Figures 75 and 76 show the epigyna of two specimens of *P. arenicola* from England and Germany. For more information about this species, see Tongiorgi, 1965.

Pardosa aeronauta (Contarini)

Lycosa aeronauta Contarini, 1847, Atti Ist. Venezia Sci. Lett. Art., 6: 441–444.

From the short note of Contarini it is impossible to identify the species. Thorell (1872, p. 292) gives a short description of this species based on some data from Ninni. Thorell regards *P. aeronauta* as probably belonging to the *P. monticola* group. Since Thorell's species is impossible to recognize

from the description, I regard this name as a *nomen inquirendum.* According to Contarini the species is abundant on the salty sandbanks of Valle Grassabò (Venezia).

Pardosa subglacialis C. L. Koch *in* Calloni

Pardosa subglacialis,—Calloni, 1890, La fauna nivale con particolare riguardo ai viventi delle alte Alpi, Pavia, pp. 139, 274, 410, 436.

Calloni says he received from Koch a communication on the existence of a new species called *P. subglacialis.* Koch never published a description of this species. The name is a *nomen nudum.*

Pardosa frigida Simon 1876

Pardosa frigida Simon, 1876, Les Arachnides de France, 3: 353, pl. 13, fig. 15, ♀. Female holotype from Faillefeu, Basses Alps, France, lost.

The reasons for considering this species distinct from *P. cavannae,* not following the later opinion of Simon, are explained in the discussion of *P. cavannae.* From the description, *P. frigida* could be a species of the group of *P. ferruginea,* but the epigynum shape is quite different. For the present I do not know any specimens of this species, and I cannot relate *P. frigida* to any of the other species of *Pardosa.* The specimens from Monte La Bioula, 3000 m, Valle d'Aosta: Gran Paradiso National Park, determined by Di Caporiacco (1928), were juvenile and the identification doubtful. I regard *P. frigida* as a questionable species.

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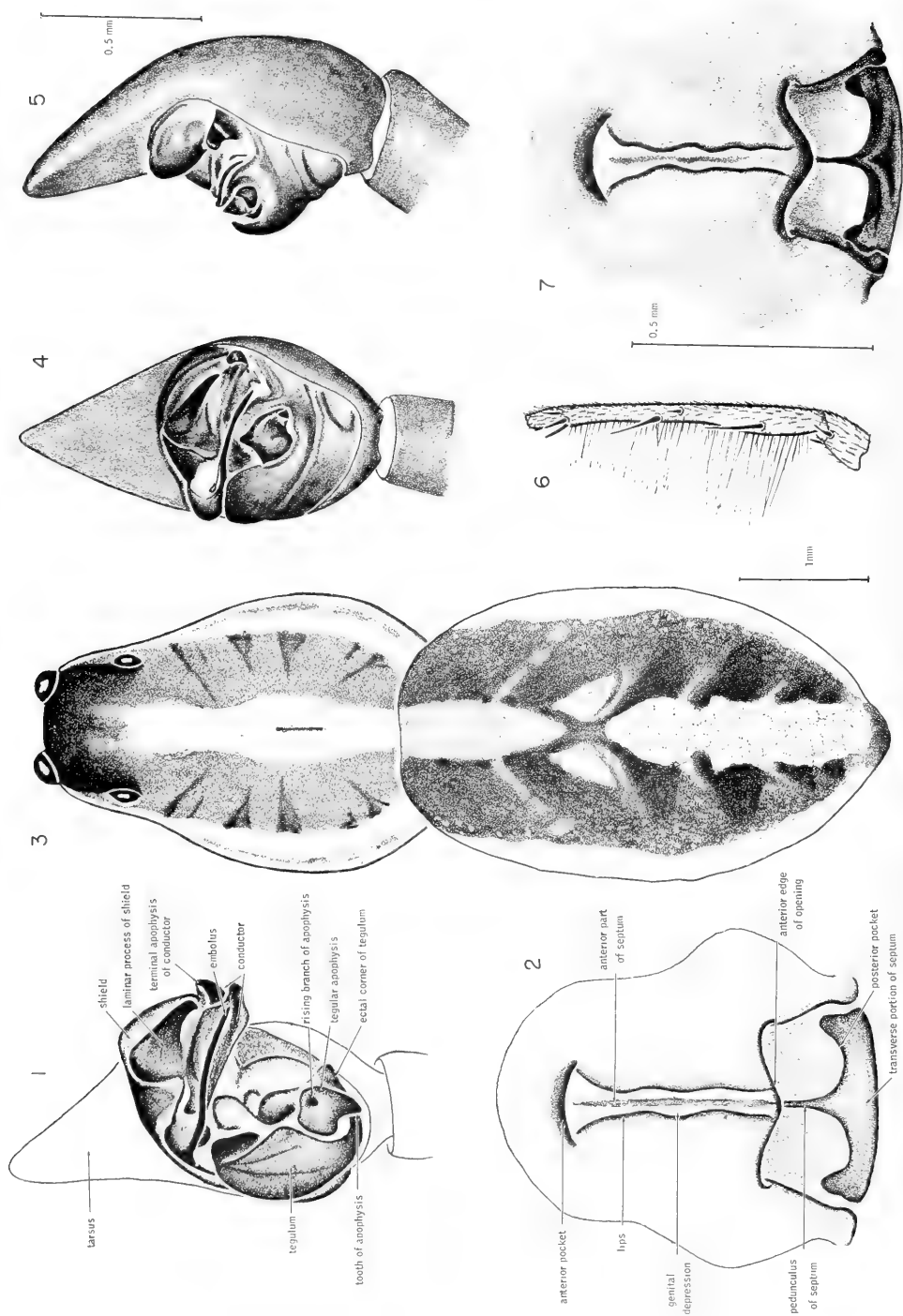
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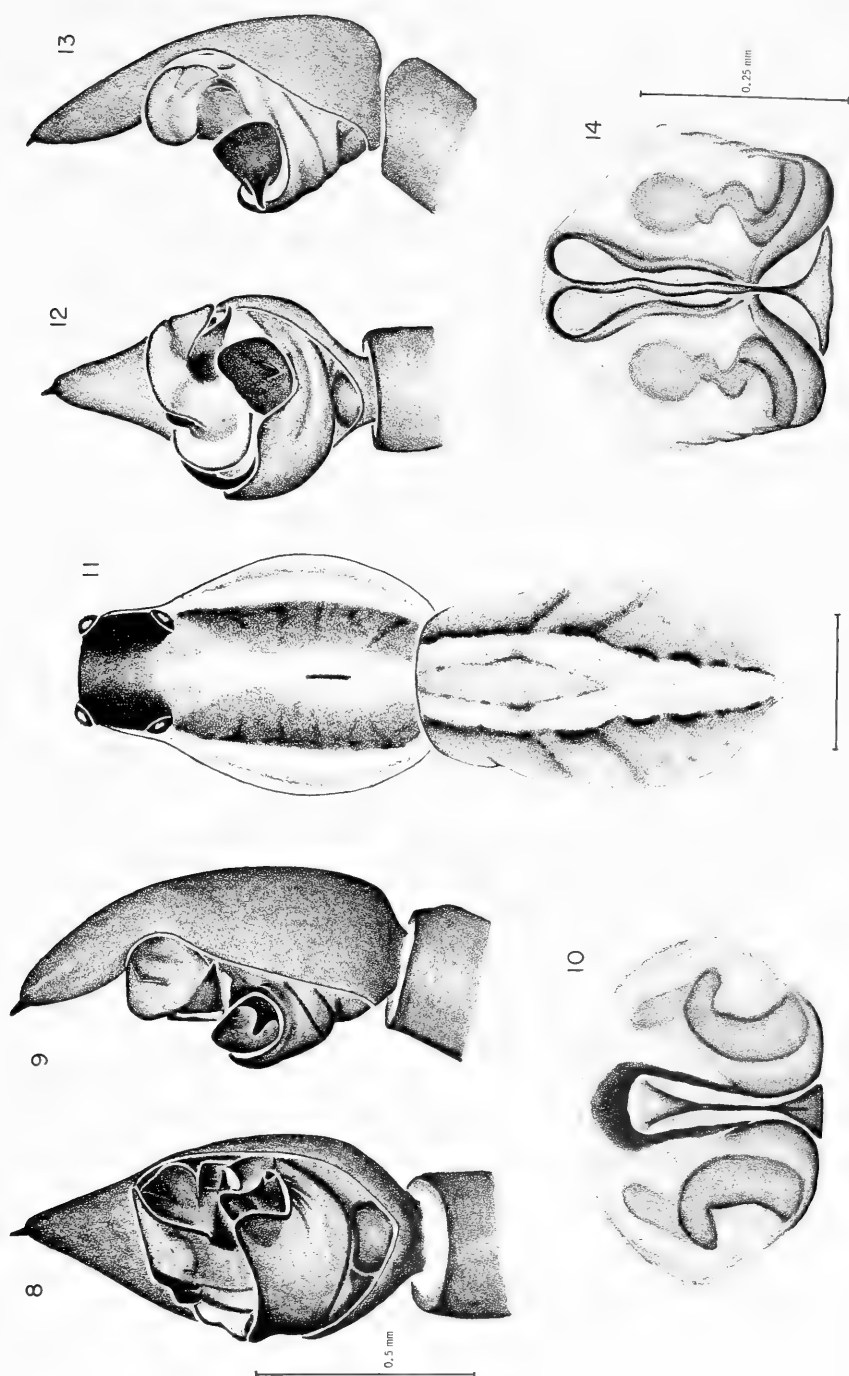
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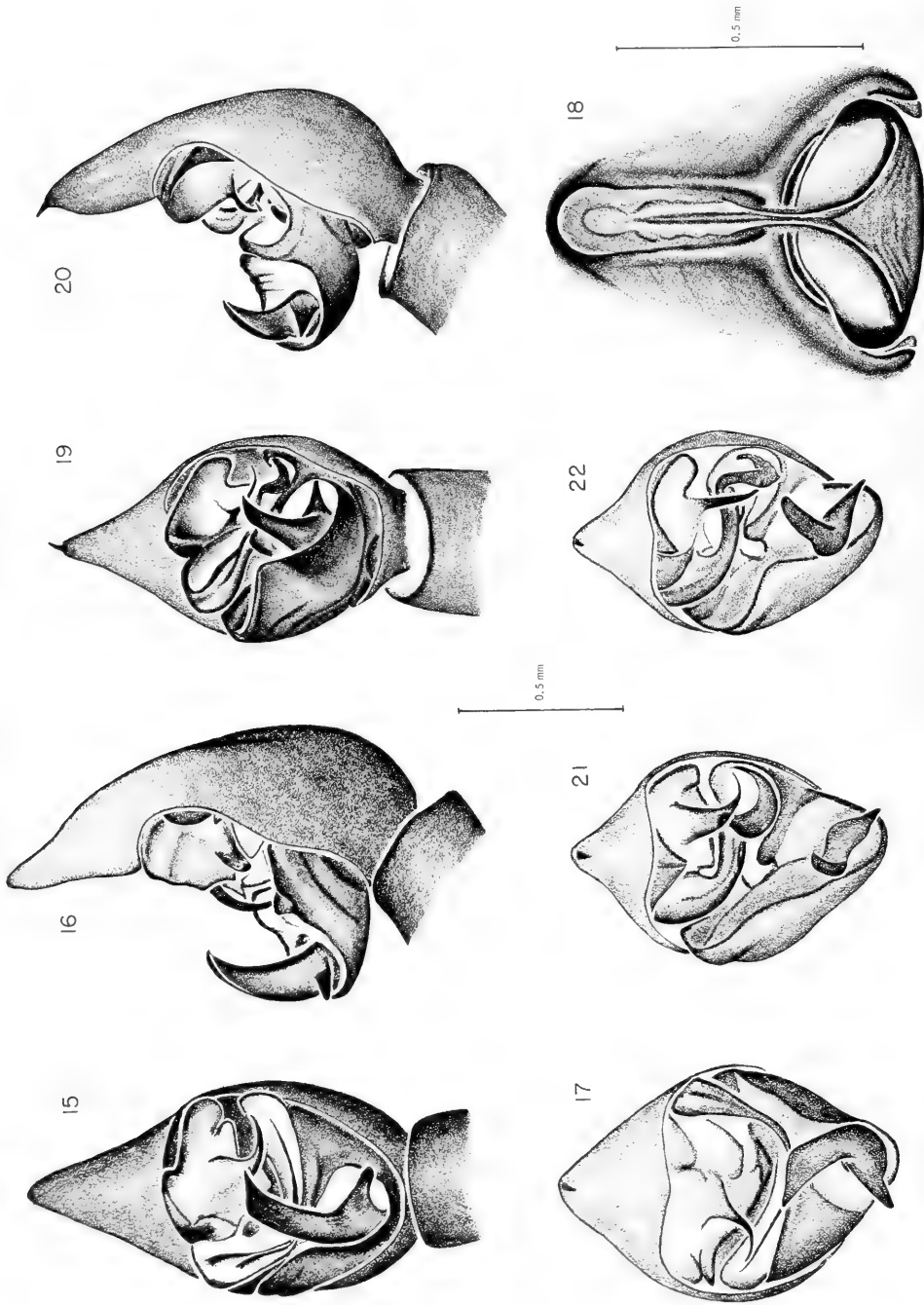
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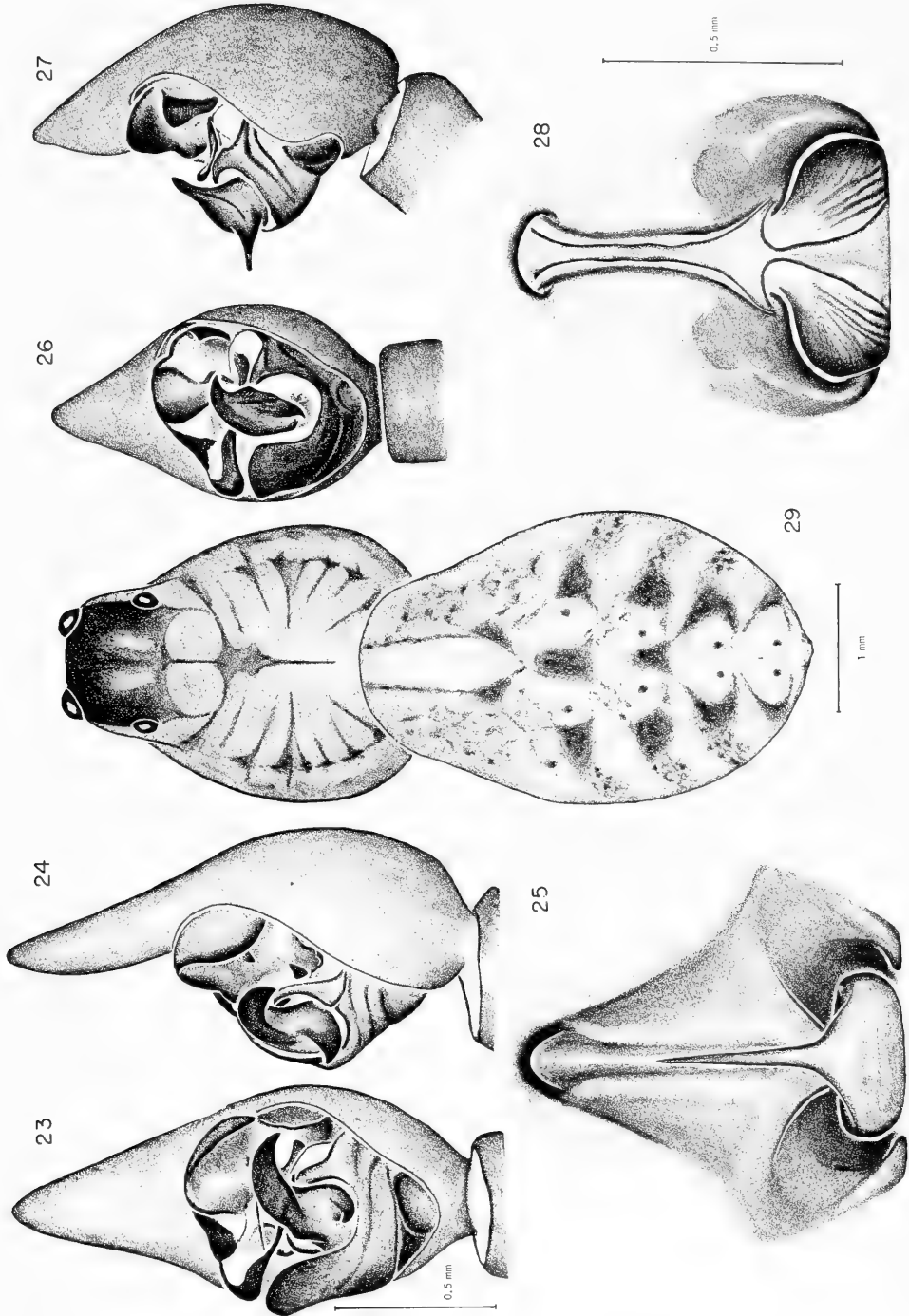
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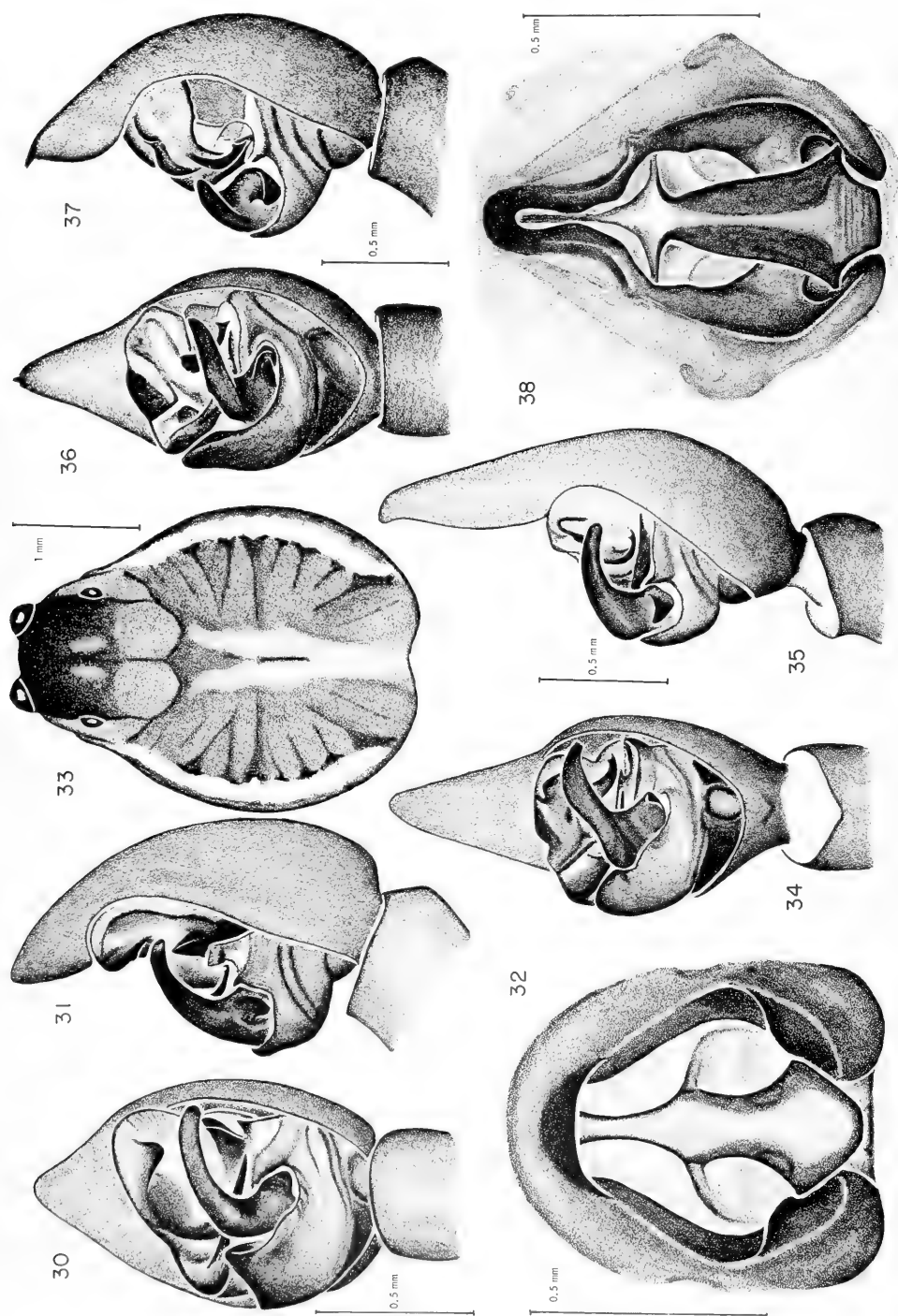
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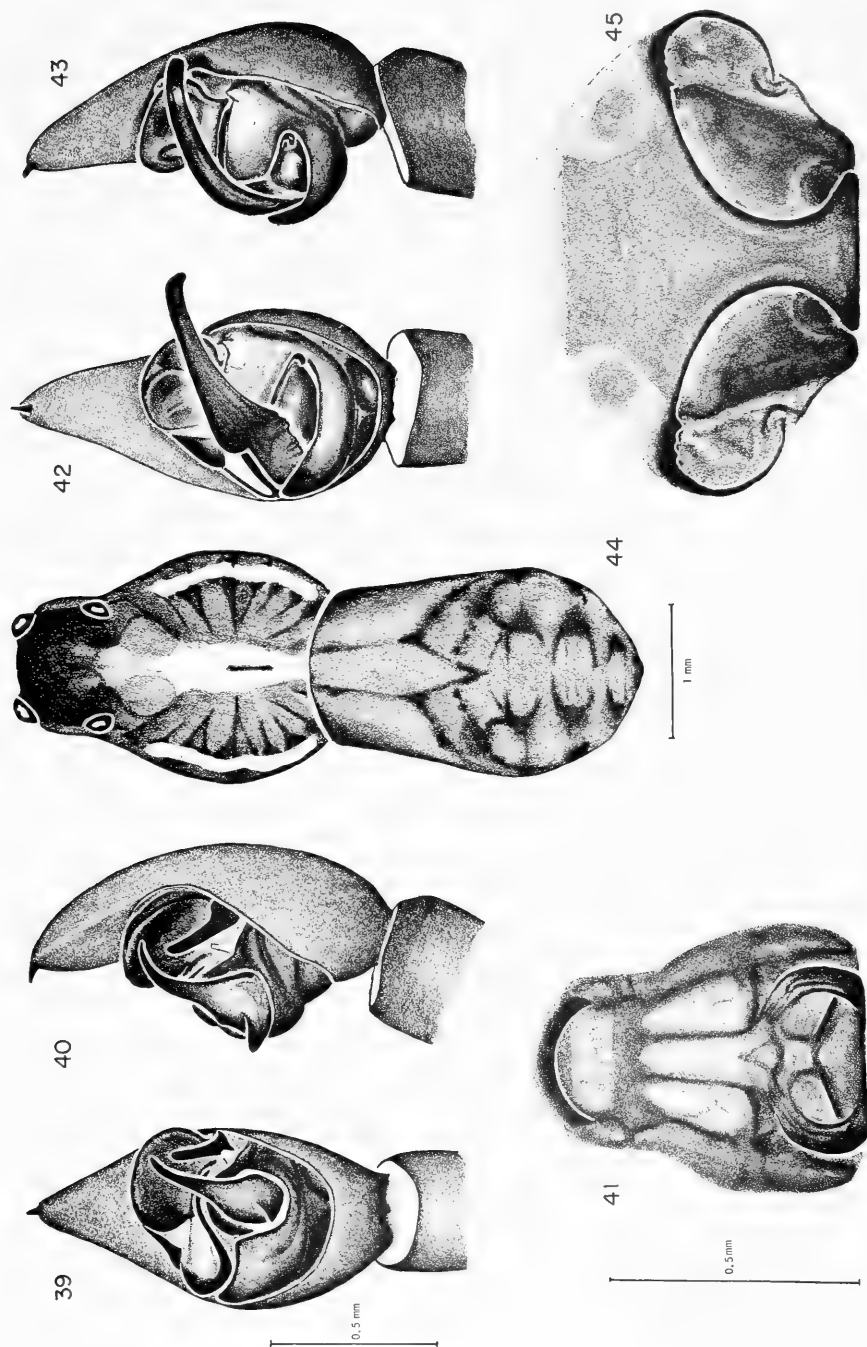
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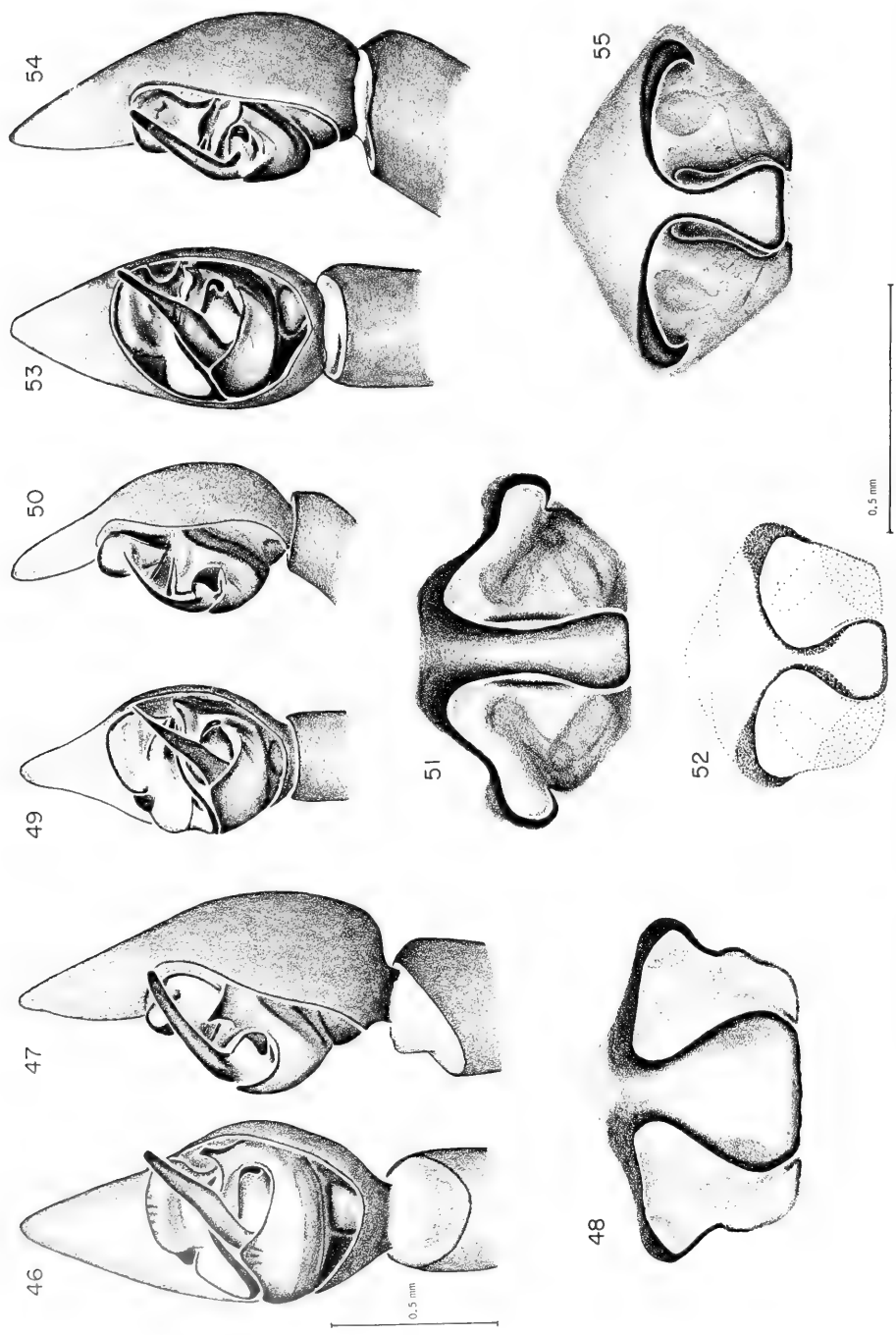
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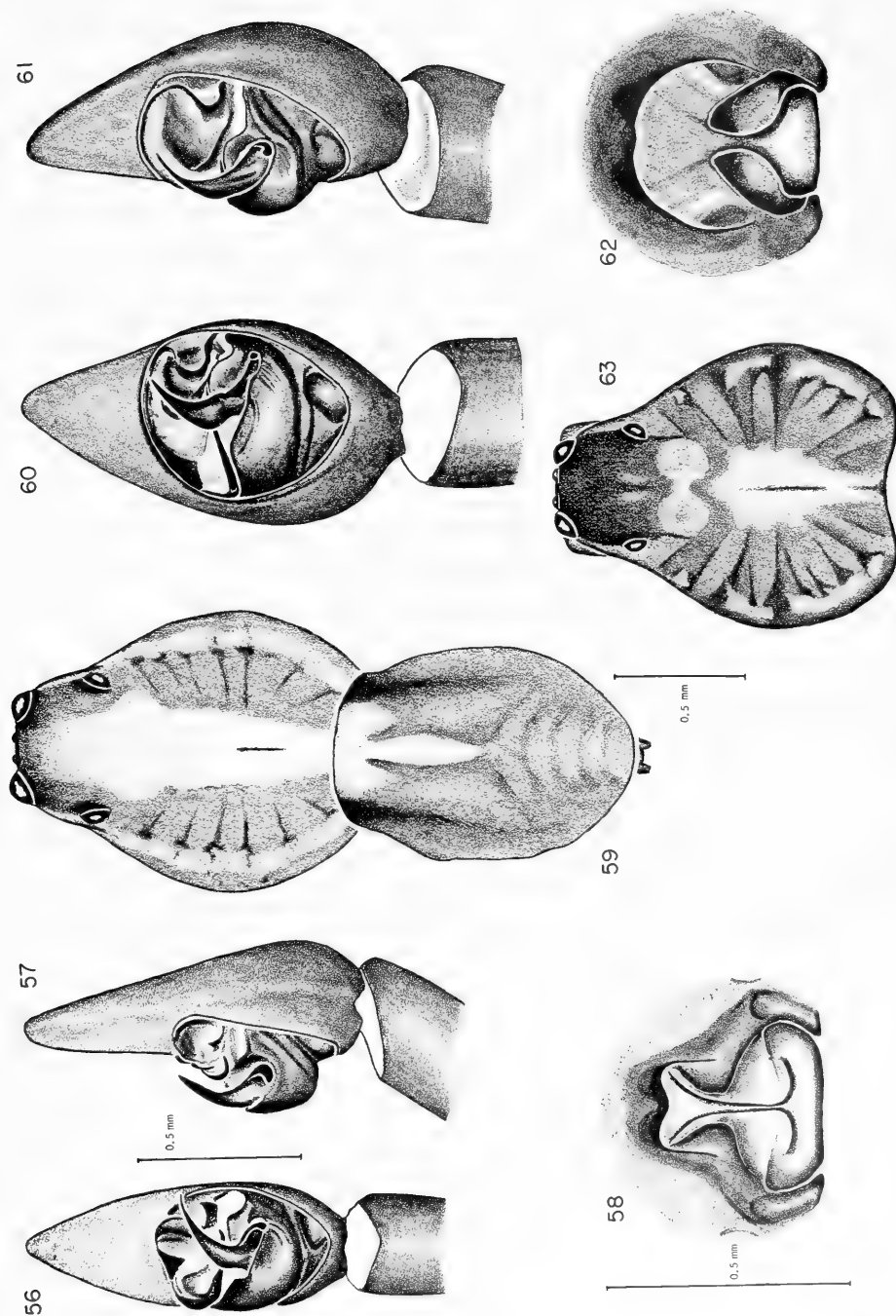
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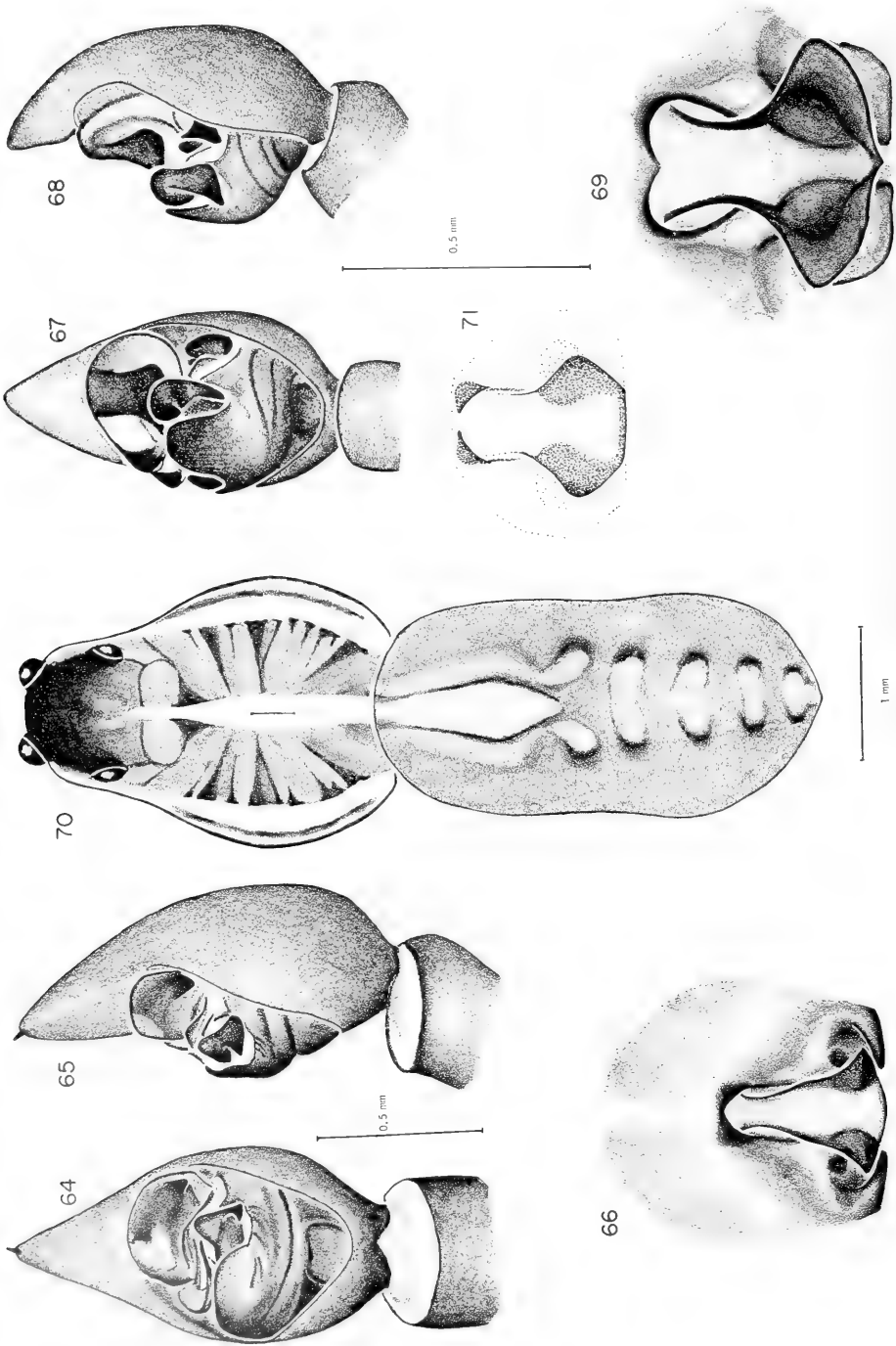
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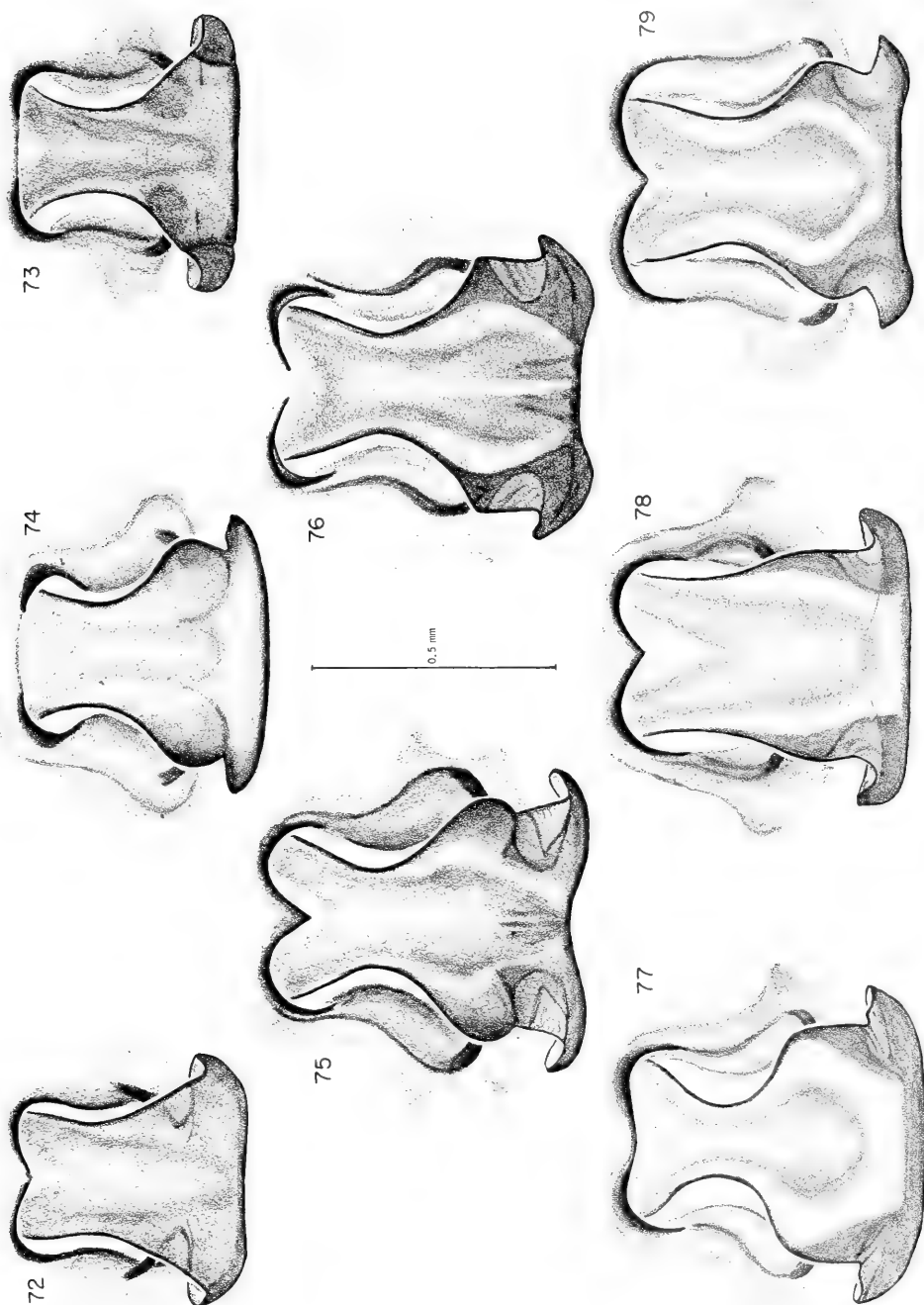
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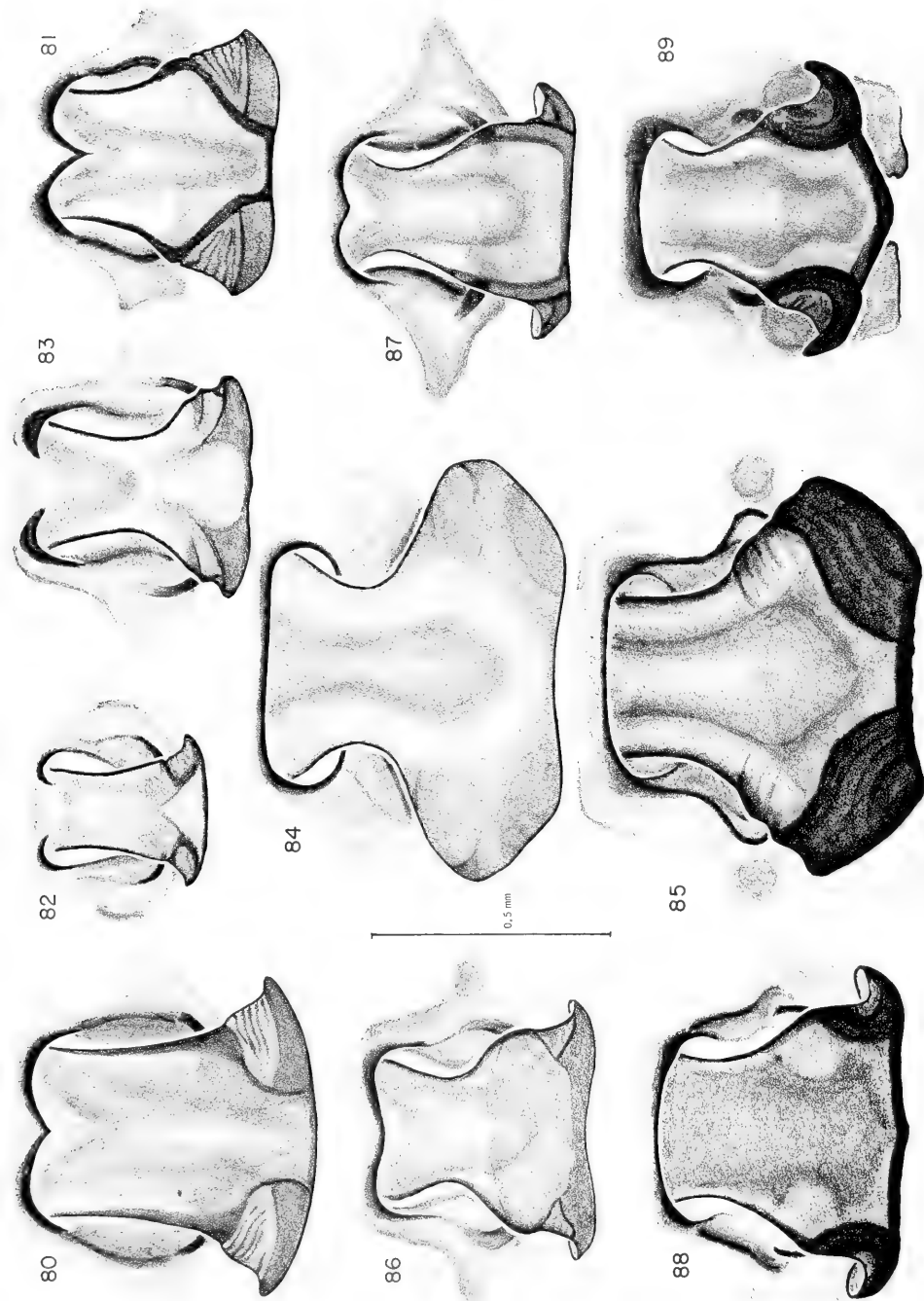
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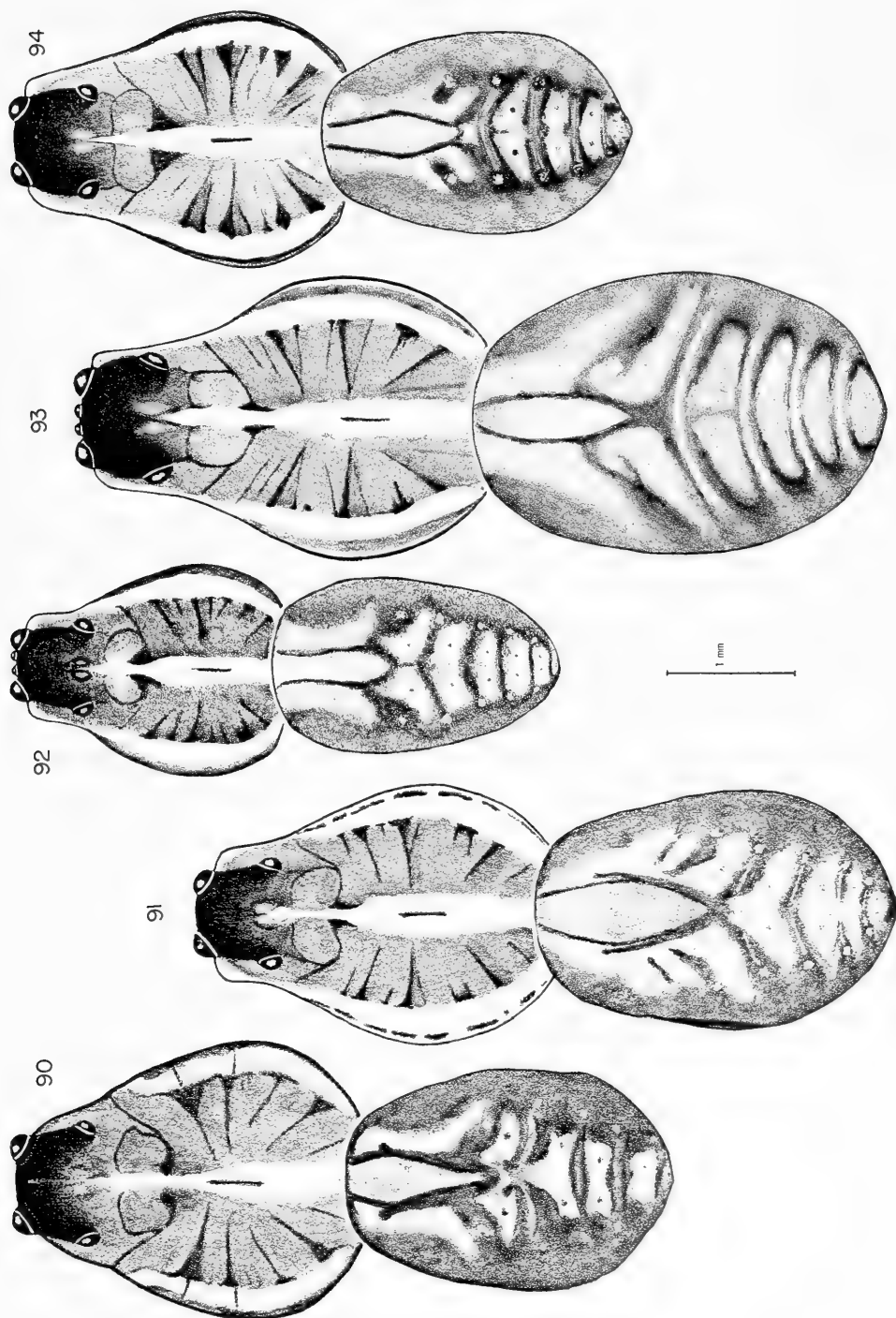
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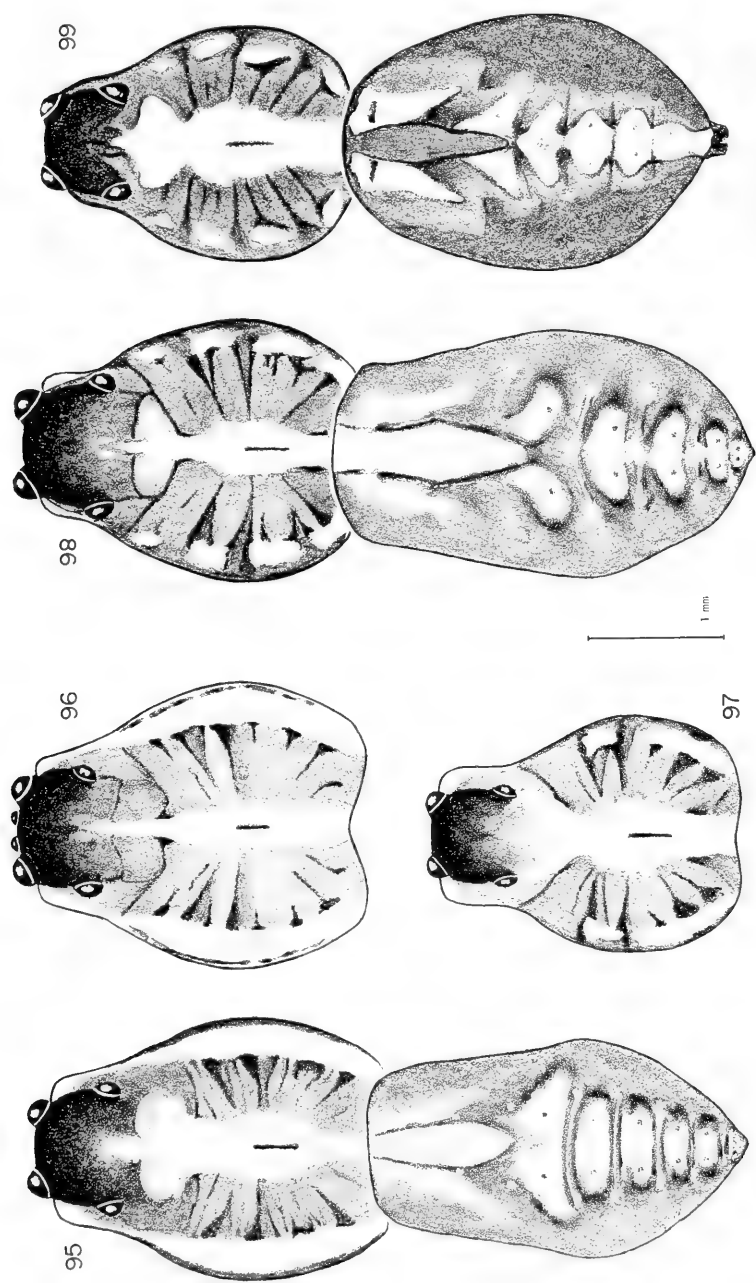
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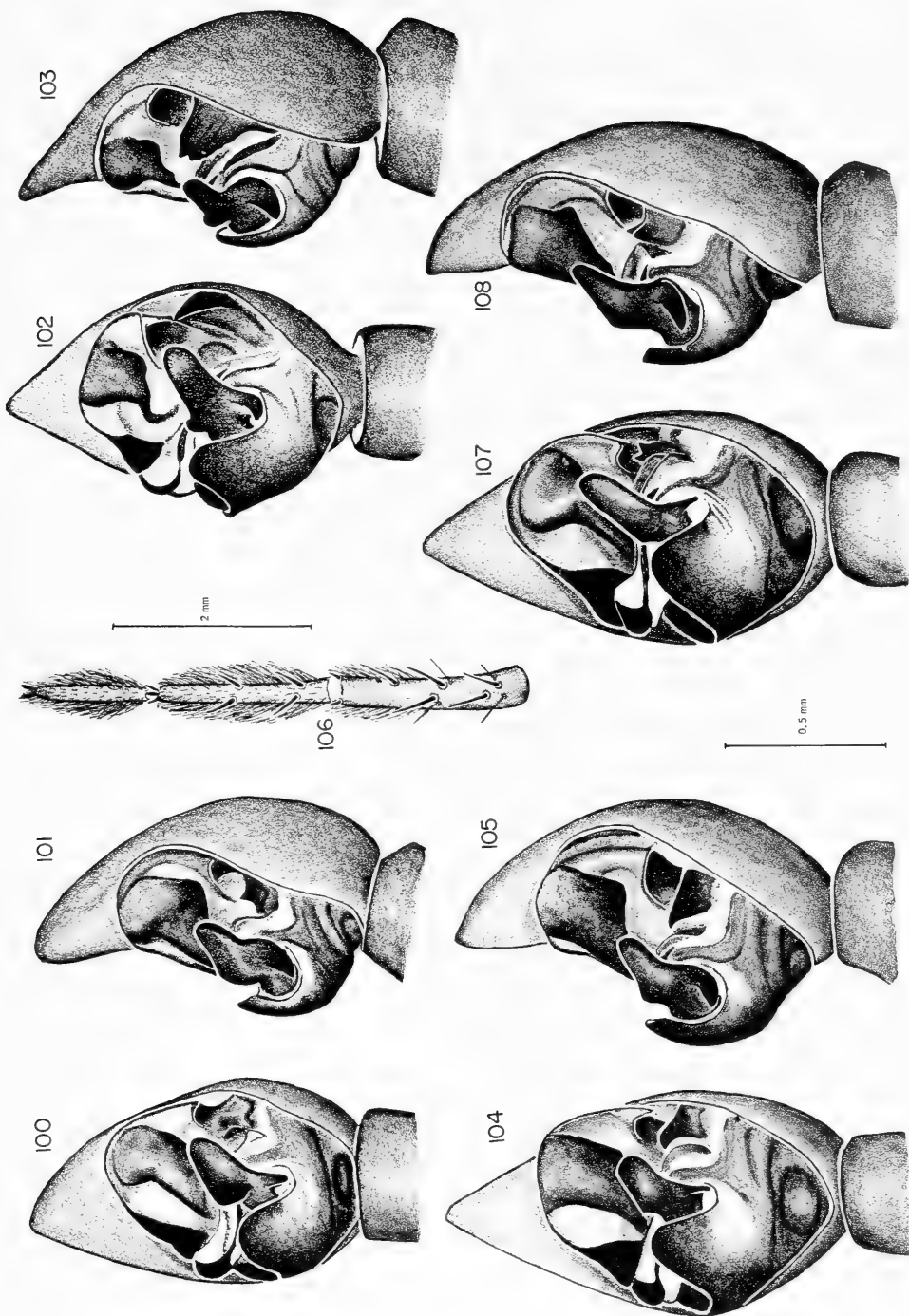
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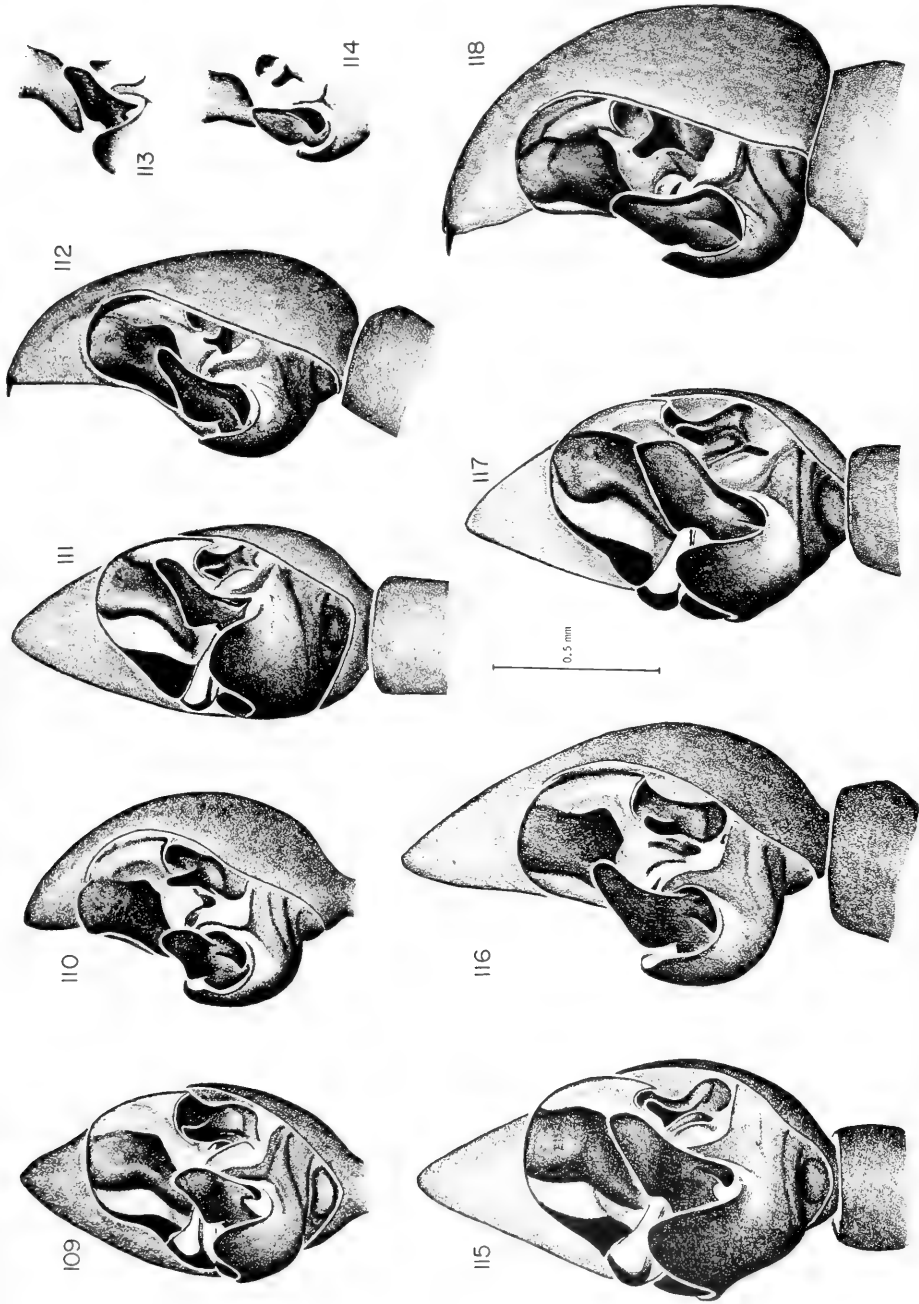
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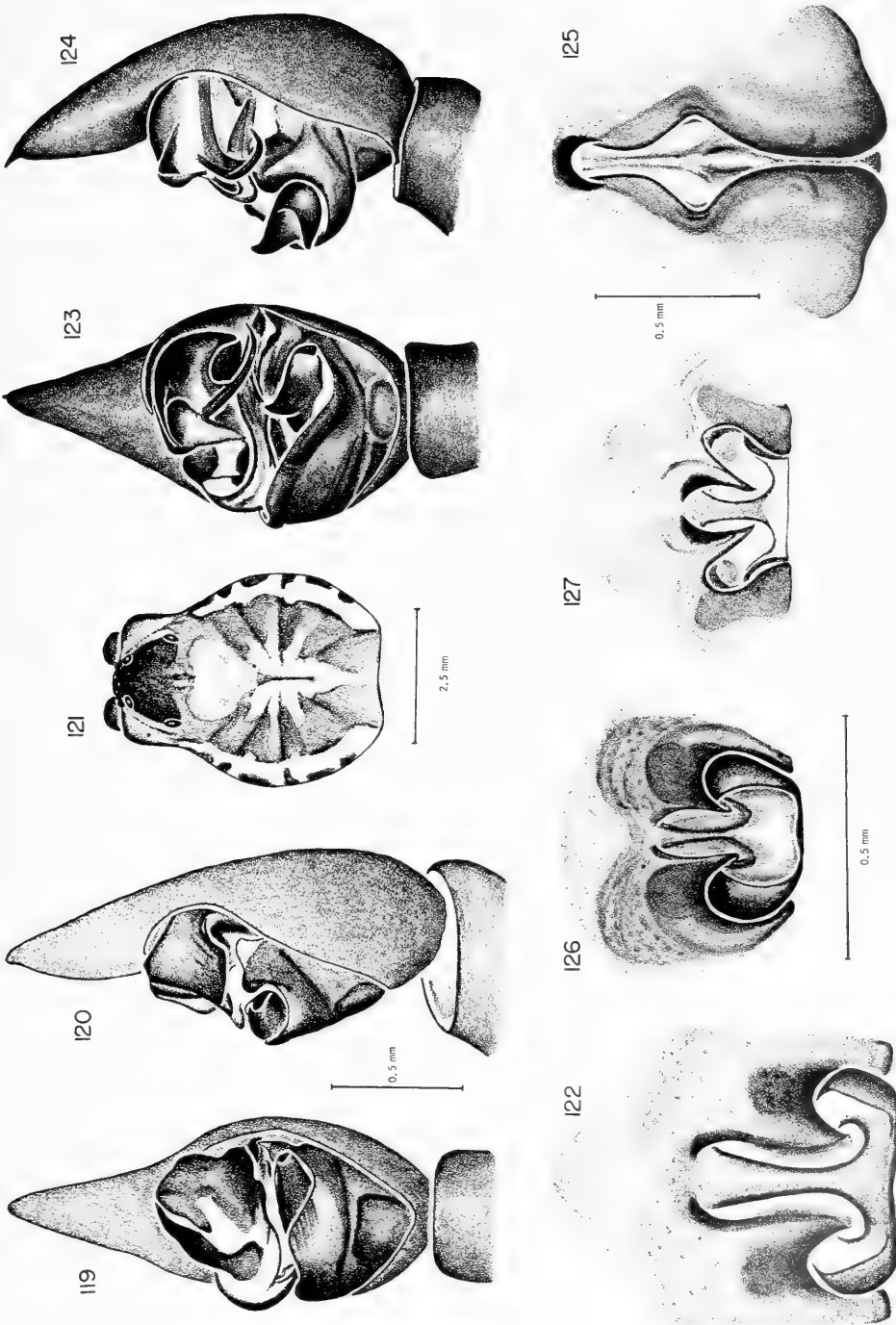
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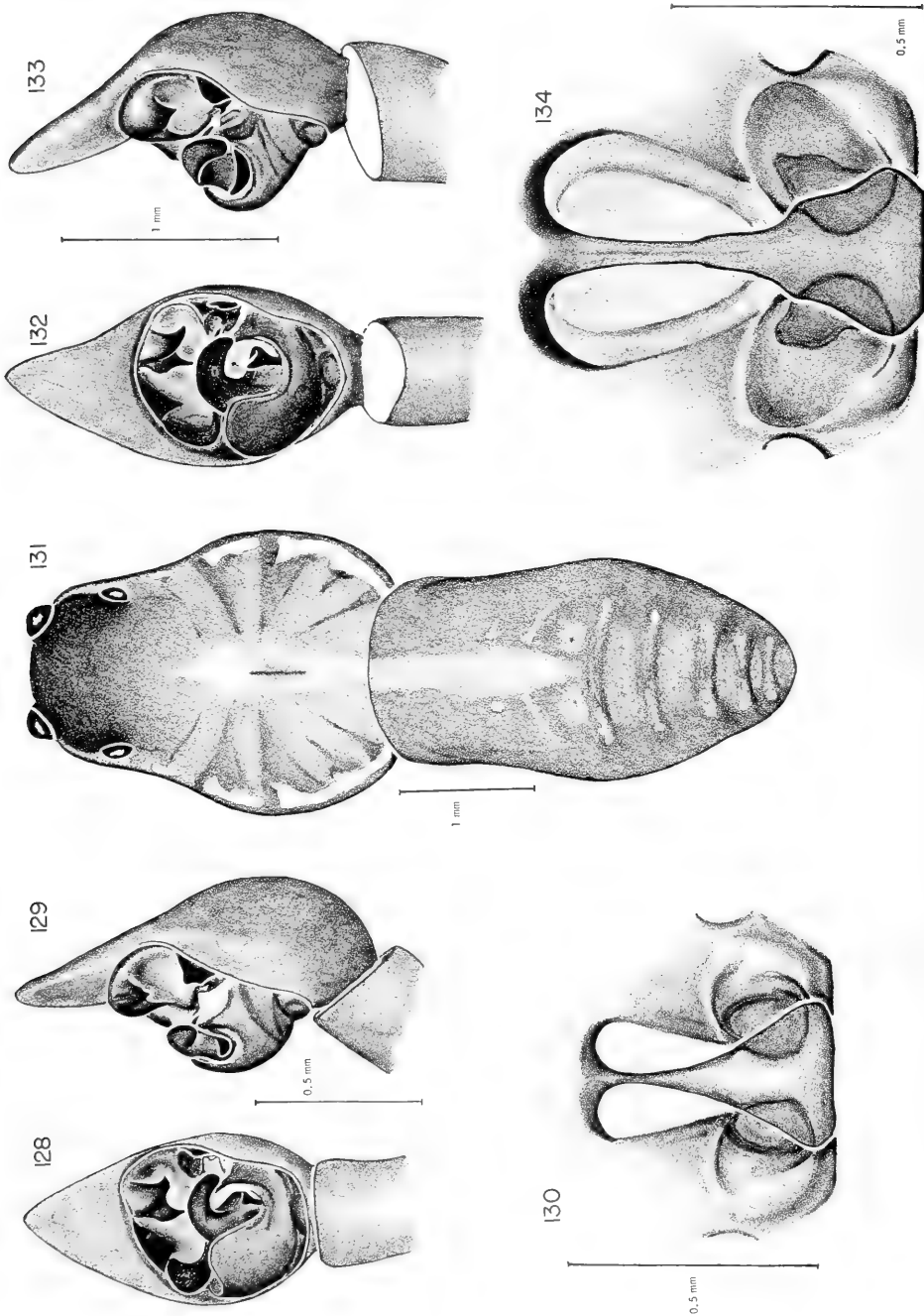
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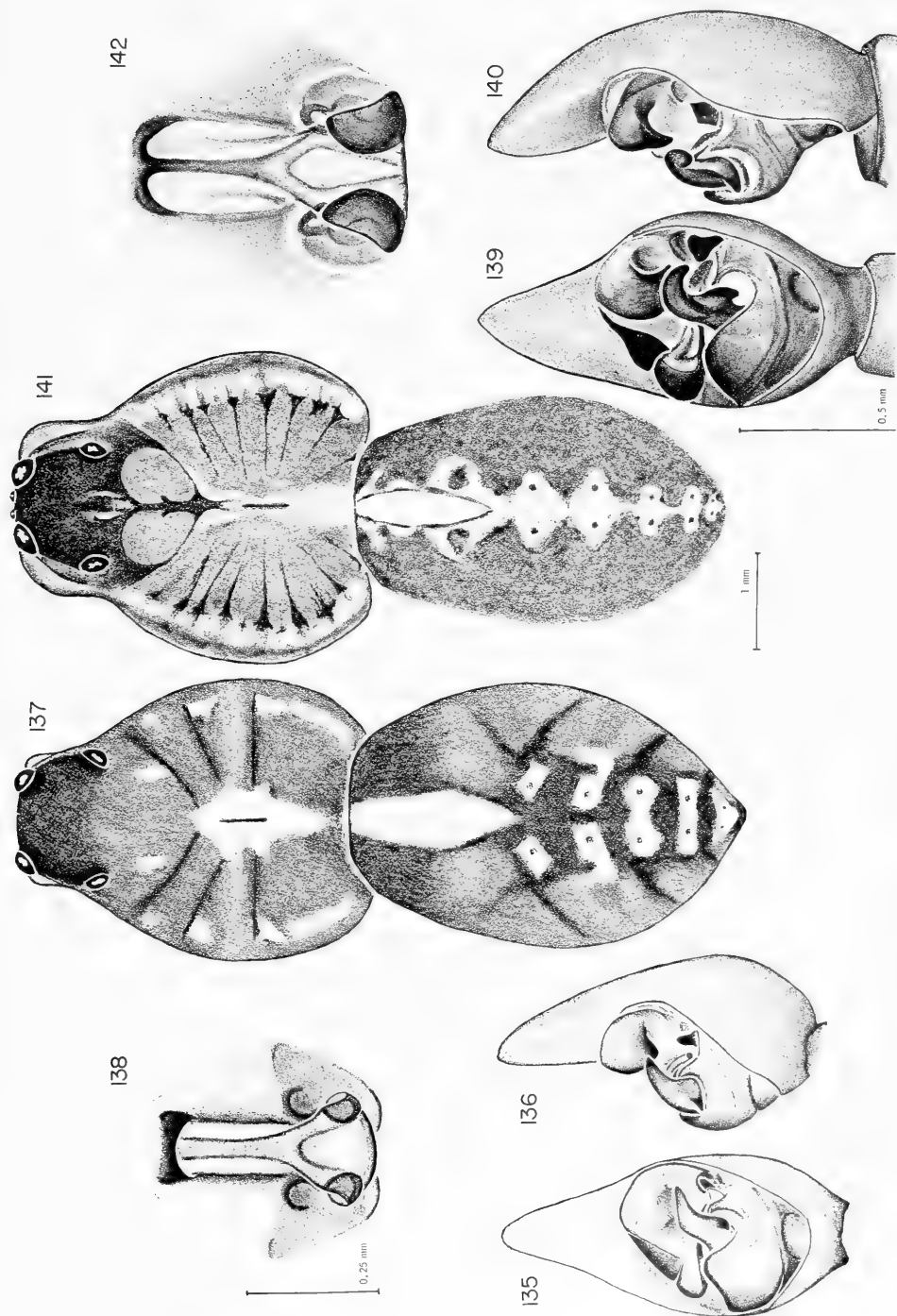
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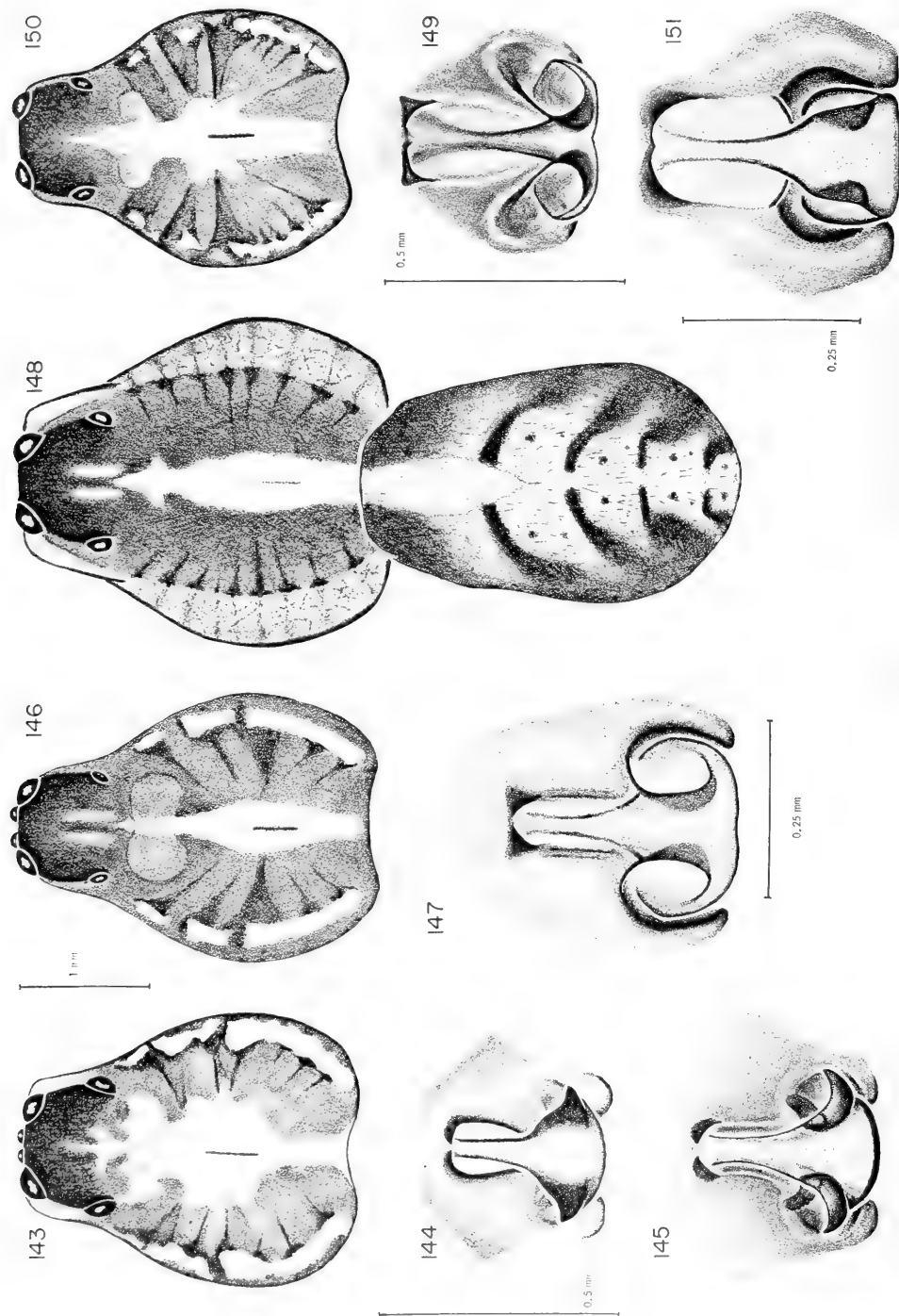
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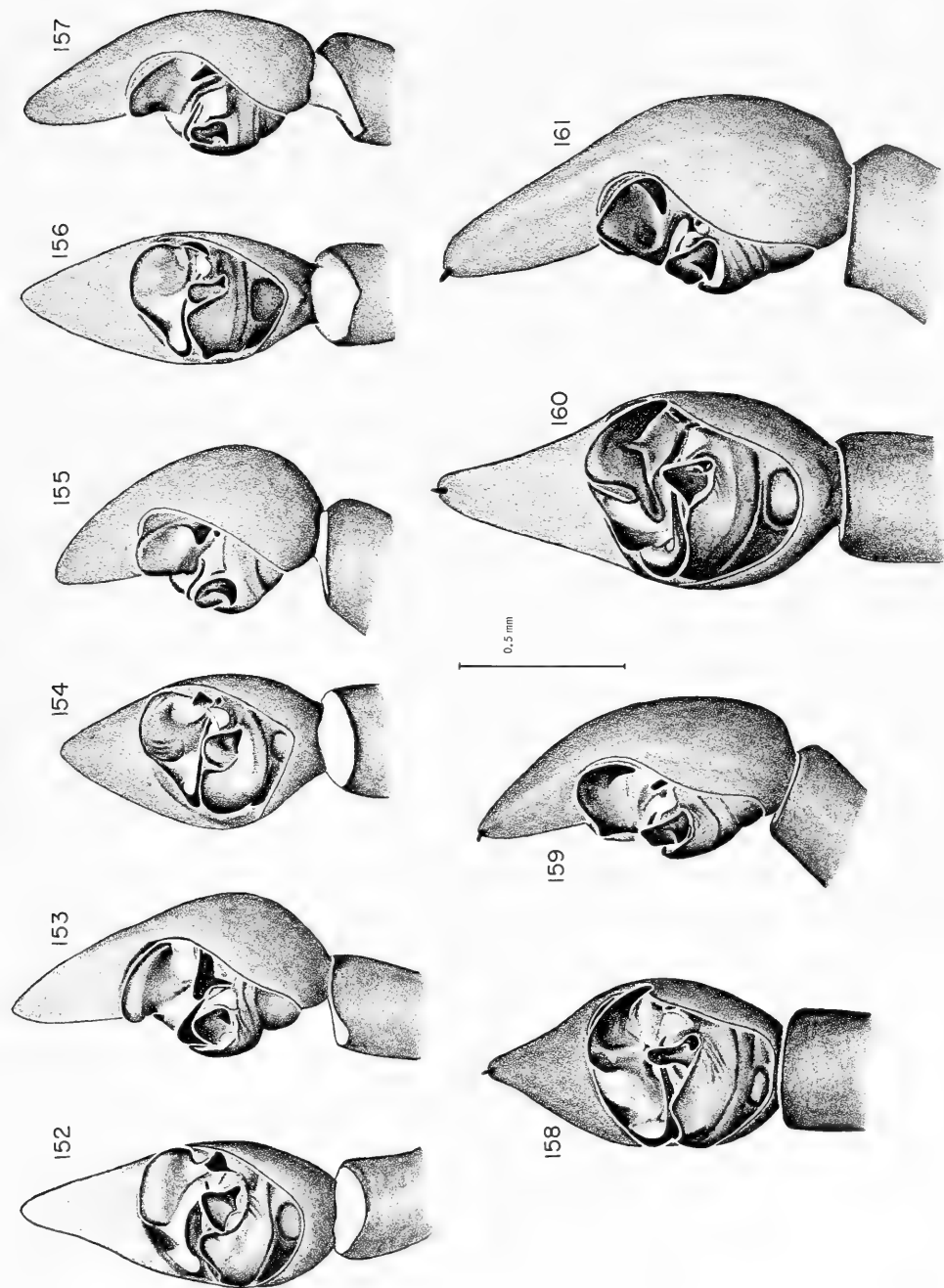
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Wolf Spiders of the *Pardosa monticola* Group (Araneae, Lycosidae)

by PAOLO TONGIORGI

Museum of Comparative Zoology, Cambridge, Massachusetts
Istituto di Biologia generale, Università di Pisa, Italy

WOLF SPIDERS OF THE *PARDOSA MONTICOLA* GROUP (ARANEAE, LYCOSIDAE)

PAOLO TONGIORGI

Among the species of the genus *Pardosa*, those of the *monticola* group are easily distinguished from all the others, but it is difficult to distinguish the different species within the group. Identification of females is often uncertain because of their extreme similarity and great variability. In contrast, under careful examination, the males reveal some distinctive features that allow quick identification. The lack of a revision of the group makes identification still more difficult as the literature is scattered and the different authors have used different taxonomic criteria.

Having large collections available from several European localities, I have tried to fill the need for a revision. The material was partly collected by myself and others, and in part kindly lent by the curators of the museums of Genoa and Florence, Italy, and from the Museum of Comparative Zoology at Harvard University. During my study of various collections, I found fifteen species in the group and several of doubtful taxonomic status. Because of the difficulty of recognizing the species belonging to the *monticola* group on the basis of the original descriptions, undoubtedly some species were missed. Often it was difficult to match males and females; when in doubt I followed earlier authors.

For the different species I listed only references to works that have useful drawings or are of particular interest. For additional references, the bibliographic works of Bonnet (1958) and Roewer (1954) may be consulted. I based the geographical distributions of the species of the *P. monticola* group on the data furnished by these authors; therefore, I want to emphasize that the given distributions are only tentative. The distribution assigned to many species in the literature seems to be much larger than it actually is because many specimens have been misidentified. Owing to the close resemblance of many species of the *monticola* group, specimens of less well-known species and probably also representatives of new species have been wrongly labeled as species already described. It was found that there are many closely related species in limited, often adjacent, areas.

The drawings of the left male palpus illustrate the ventral and ventrolateral views. In the ventrolateral view the palpus is rotated about 60°, a position that shows the terminal apophysis equally well in all species.

The descriptions and the drawings of the body are based on female specimens because the color pattern may be a useful distinctive character for females. The male is, as a rule, similar, but often darker and less distinct. If the male differs for some other characters it is pointed out. Only the external view of the female genitalia was drawn. Some authors have used the internal genitalia (vulva) as a diagnostic character (Dahl, 1908; Dahl and Dahl, 1927; Kratochvil, 1935). However, in this group at least, the internal genitalia do not furnish enough

clear differences. When considerable variability occurred, or it was otherwise necessary, I provided more than one drawing, selecting examples, as far as possible, from the same population. Whenever possible, specimens were selected to represent the mean of the specific variability. I made little use of measurements because in my experience they are very similar in the different species. Also the ratios used by some authors are in my opinion of little or no use, because their variability is so large that they overlap completely.

I have followed Holm's terminology (1947) in naming anatomical parts of the male and female genitalia. Septum means the wide sclerotized shield that, in this group, nearly covers the epigynal hollow. The anterior pockets (epigyntvärficka of Holm or Quertaschen of Järvi, 1905) are the two pockets at the anterior edge of the septum.

The apophyses of the male palpus are two: the tegular apophysis, large and easy to see, is placed about mid-ventrally in the bulb; the terminal apophysis is located on the external side ventrolaterally in the bulb (left side on the left palp and vice versa).

Finally, I wish to stress that the key to identification of females, and the descriptions and drawings, fit the mean of each species. It is possible that a certain specimen can hardly be recognized as belonging to one or the other species; by using numerous specimens, especially of males, one can minimize wrong identifications. In several instances, the specific name is followed by another name in parentheses, e.g. *P. agrestis* (*pseudoagricola* Dahl). I wish to make clear that this does not indicate a subspecies, but only emphasizes a particular aspect of body pattern by reference to a familiar name. Some authors have, indeed, distinguished several subspecies in highly variable species. The validity of such systematic categories is doubtful but the names introduced in the literature are useful to recognize different "forms." Due to the availability of specimens, classification and

relations with the other species are more certain for species of western Europe than for those found in other regions. For species of which I was able to examine only one or few specimens, the distinctive characters I used must be considered tentative.

KEY TO SPECIES

Some of the species of the *monticola* group have been already described (Tongiorgi, 1966); therefore, I refer to that paper instead of repeating the same figures. In the keys and in the text, "Fig." capitalized, refers to this paper, "fig." in lower case type, to my previous paper. *Pardosa angusta* Denis is included in the key, but not in the text. I was not able to examine this species, which, according to Denis (1956), belongs to the *P. monticola* group.

The species of the *Pardosa monticola* group are distinguished from other species of the *Pardosa* genus mainly by the shape of the genital organs. The males have the tarsal article of the palpus rather stout, generally with a short point. The tegular apophysis is spatulate or finger shaped and apically blunt. The tegulum, on the palpus observed from the side, somewhat projecting. On the females the septum is a trapezoidal plate covering the whole genital depression.

20. Legs evenly colored, not annulated. Lateral carapace bands broken by two fine radiating lines into three parts of equal length (Fig. 18). Epigynum with the edge of the anterior pockets as in figures 75, 76 _____ *P. arenicola*
– Legs dark, generally annulated. Partition of lateral carapace bands not clear; crossed by two thin lines (fig. 90). Epigynum with the edge of the anterior pockets as in figures 88, 89 _____ *P. blanda* (part.)
21. Septum longer than broad (or sometimes as long as broad) _____ 22
– Septum broader than long _____ 24
22. Edges of the septum almost parallel or slightly enlarged posteriorly _____ 23
– Edges of the septum clearly parallel on the anterior half. Edge of the anterior pockets as in Figure 26; legs annulated _____ *P. incerta*
23. Median band fusiform, pointed anteriorly. Epigynum with the edge of the anterior pockets as in figure 83; legs light, more or less annulated _____ *P. monticola*
– Median band truncate in front and a little enlarged on the thorax _____ *P. angusta*
24. Septum clearly much broader than long. Posterior lateral angles generally prominent, either obtuse or pointed _____ 25
– Septum becoming larger posteriorly with more or less sinuous sides. Edge of the anterior pockets even, as in *P. blanda* or *P. palustris* (except *P. plumipes*) _____ 27
25. Legs, especially femora, dark; posterior legs sometimes annulated. Epigynum with the edge of the anterior pockets as in figures 88, 89 and posterior lateral angles sometimes outside and sometimes pointing anteriorly _____ *P. blanda* (?*P. albata*)
– Legs light; femora with dorsal blotches sometimes extending to their undersides. Other legs uniform reddish or yellow-brown or more or less annulated _____ 26
26. Posterior angles of septum obtuse, often wrinkled and prominent. Septum with longitudinal deep groove about ⅔ its length. Edge of the anterior pockets as in figures 84, 85 _____ *P. palustris*
– Epigynum as in Figure 31 _____ *P. consimilis*
27. Sides of septum subparallel, expanded anteriorly, with the posterior angles more or less blunted and often a little wrinkled (figs. 80, 81). (Distinguished from *P. palustris* by differently shaped edge of the anterior pockets) _____ *P. mixta*

– Sides of the genital plate rather sinuous with the posterior angles generally beak-shaped _____ 28
28. Edge of the anterior pockets as in Figures 24, 32. Posterior lateral angles rather prominent _____ 29
– Edge of the anterior pockets different ____ 30
29. Epigynum as in Figure 32. Metatarsi IV rather dark _____ *P. plumipes*
– Epigynum as in Figure 24. Metatarsi IV not darker than other legs _____ *P. pontica*
30. Legs annulated _____ 31
– Legs without annulations or with very pale annulations on some segments only ____ 32
31. Legs more or less annulated. Femora with dorsal dark marks extending to ventral side (figs. 72–74) _____ *P. agrestis* (part.)
– Femora with dorsal marks and uniformly darkened ventrally. Distal half of metatarsi dark. Epigynum as in Figure 30 __ *P. olympica*
32. Legs without annulations, or annulations on metatarsi III and IV only. Femora with dark marks on the dorsal side only. Epigynum as in Figure 25 ____ *P. purbeckensis*
– Legs light yellow. Some pale annulations on the dorsal sides of femora and tibia. Legs and body with numerous white hairs. Epigynum as in Figure 29
_____ *P. ilguenensis*
33. Lateral light bands of carapace broken ____ 34
– Lateral bands continuous _____ 36
34. Septum about as broad as long; lateral sides S-shaped. Edge of the anterior pockets as in figures 77–79; legs clearly annulated _____ *P. agricola*
– Septum broader than long _____ 35
35. Legs annulated. Edge of the anterior pockets as in figures 86, 87; abdominal pattern yellow-red, rather pronounced (fig. 99) _____ *P. torrentum*
– Legs scarcely annulated. Sides of the septum regularly enlarged, only a little sinuous. Edge of the anterior pockets as in figures 72–74 _____ *P. agrestis* (part.)
36. Septum much longer than broad, as in Figure 28 _____ *P. occidentalis*
– Septum broader than long _____ 37
37. Epigynum as in figures 84, 85. Lateral light bands very broad, reaching sides of carapace. Posterior sides of abdomen thickly clothed with white hairs _____
_____ *P. palustris* (part.)
– Epigynum as in figures 72–74. Between the sides of carapace and the lateral light

bands is one thin, dark band. Abdomen without white hairs except the usual pattern .... *P. agrestis*

Pardosa ilguenensis Nosek
Figures 3–5, 20, 29

Pardosa ilgünensis Nosek, 1905: 142–143, pl. 5, figs. 20, 22a, b, ♂ ♀. Two males and one female lectoparatype from Ilgyn, Turkey, in the Naturhistorisches Museum, Vienna, examined. One male lectotype, here designated.
P. ilguenensis,—Roewer, 1954: 164. Bonnet, 1958: 3377.

Description. Female carapace brown. Light median band yellow and spindle-shaped. Lateral bands yellow, wide, continuous, separated from the margins of carapace by a dark band of rather faint brown spots. Legs yellow. Some pale brown rings on upper sides of femora and tibiae.

Male carapace darker than in female. Light median band spindle-shaped. Yellow lateral bands continuous, only a little wider than the median one. Legs yellow; femora with dorsal blotches, other segments uniform.

Tibiae and metatarsi of the first two pairs of legs clearly thicker than the corresponding segments of other legs. These two segments are covered thickly with short hairs that form a scopula ventrally, and contribute to the characteristic appearance of the legs. The ventral spines on the tibiae and metatarsi are very short. The whole body is covered with white pubescence. Male palpus as in Figures 3–5. Femora slightly brown striped, other segments pale yellow. The terminal apophysis, shaped as a triangular tooth, looks conical from the side.

Remarks. The male and female probably belong to the same species, but this is not certain. The male of this species is distinguished by the structure of the palpus and by the characters of the first two pairs of legs. The female, judging by the carapace pattern and the shape of the septum

is closely related to *P. incerta.* The legs show differences in annulation. Having only one female, I cannot make any comparison with the other species. Figure 5 shows the tegular apophysis of the paratype of *P. ilguenensis.* It is slightly different from that of the type.

Distribution. Turkey: Ilgyn.

Pardosa incerta Nosek
Figures 1–2, 26

Pardosa incerta Nosek, 1905: 139–140, pl. 5, figs. 17, 23, ♀. Female holotype from Erdschias-Dag (Erdjies-Dagh) in Asia Minor, in the Naturhistorisches Museum, Vienna, examined.— Roewer, 1954: 164. Bonnet, 1958: 3377.
Lycosa incerta,—Giltay, 1932: 19, fig. 13, ♀.

Note. In a footnote, Nosek (1905, p. 142), mentions some females found in Erdjies area. These females are preserved, in the same vial, with the types of the *Pardosa pentheri* Nosek and among them I found also a male of one *Pardosa* belonging, with the above mentioned females, to the *P. monticola* group. Actually *P. pentheri* belongs to the genus *Alopecosa* and is exactly like *Lycosa cursoria* var. *insignis* described by Nosek on page 138, the type of which I examined. This *Alopecosa* is probably identical to *Tarentula cursor elatior* described by Kratochvil (1935, p. 19, fig. 14, ♀) from Vales, Macedonia. On page 142, concluding the description of *Alopecosa pentheri*, Nosek says that this species must be regarded as very closely related to *Pardosa plumipes* Thorell. While the male of *Alopecosa pentheri* is quite different from that of *P. plumipes*, the male preserved with the females has long hairs on the first pair of legs, just as *P. plumipes* has. It is clear that Nosek confused the two specimens, or at least added to the description of *Alopecosa pentheri* a character that does not exist in this species. I made drawings of this male and the epigynum of one of the females that seem to me to be identical with *P. incerta*; is is nevertheless yet to be confirmed that this male really matches the

female of *P. incerta.* As Nosek's drawings are sufficient, I did not make drawings of the type specimen of *P. incerta.*

Description. Carapace dark brown. Median and lateral bands yellow, covered with white pubescence. Median band spindle-shaped, anteriorly very sharp; lateral bands continuous, as wide as median, separated from margins of carapace by a dark band. The carapace pattern is similar to that of *P. monticola* (fig. 94). Legs yellow-brown. All segments clearly annulated. Abdomen yellow-brown with very pale pattern. Epigynum as in Figure 26.

The male is similar to the female, but darker. Legs: femora with dorsal annulations, more or less uniformly darkened ventrally. Tibiae with annulations. Metatarsi probably annulated but as a result of the prolonged stay in alcohol it is difficult to judge. Metatarsi of the first legs with long hairs as in *P. purbeckensis*; tarsi and tibiae also with long hairs. The hairs have broken off in several places so that it is impossible to see their arrangement on these segments. The male palpus as in Figures 1, 2; apically the tegular apophysis leans entirely against the part of the bulb below it (shield: see Tongiorgi, 1966, Fig. 1). As the left palpus is missing, I could not see whether this character appears in both palpi. The terminal apophysis is a little tubercle, and very difficult to see. Distally the femora and patellae of the male palpi are covered with white hairs.

Remarks. Pardosa incerta is closely related to *P. purbeckensis.* The male can be distinguished by the different shape of the tegular apophysis. The terminal apophysis of *P. purbeckensis* carries a prominent little crest that, observed from the ventral or lateral side, looks as in Figures 14, 15. This crest is absent in *P. incerta* (Figs. 1, 2). The annulations on the femora, reaching to the ventral side, distinguish the female of *P. incerta* from that of *P. purbeckensis.* In this character *P. incerta* is similar to *P. agrestis.* It is possible to distinguish females of *P. incerta* from those of *P. ilguenensis* by the

annulation of the legs. Some specimens of *P. agrestis,* in the Museum of Comparative Zoology, collected in Hungary near Deliblat by Reimoser, have an epigynal septum identical to that of *P. incerta* but have the carapace pattern of the typical form of *P. agrestis.*

Distribution. Asia Minor: Erdschias-Dag 1 ♀; Erdschias area 7 ♀ ♀, 1 ♂ (Penther-Zederbauer) (Nosek Coll., NMW); Tachtoli-Dag, 440 m (Giltay, not examined).

Pardosa purbeckensis F.P.-Cambridge
Figures 14–15, 21, 25

Pardosa purbeckensis F.P.-Cambridge, 1895: 32–34, pl. 4, figs. 1, 4, 7a, 8a, 9, ♂ ♀. Male and female syntypes from Poole Harbour, England, probably in the British Museum, London.—Roewer, 1954: 172. Bonnet, 1958: 3416.

Lycosa purbeckensis,—Smith, 1907: 18, pl. 1, figs. 5a, b; pl. 4, fig. B, ♂ ♀. Locket and Millidge, 1951, p. 258, figs. 123 D, 126 A, B, 127 D, ♂ ♀. Knülle, 1954, pl. 22, figs. 4a, 5, ♂.

Description. Carapace dark brown. Median light band sometimes attenuated anteriorly, sometimes slightly enlarged as an arrow point behind the posterior eyes. Lateral bands as broad as the median one, extending to clypeus (not always in the males). (For the drawings of carapace pattern see *P. monticola.*) Legs yellow-brown. Dorsal sides of the femora with dark longitudinal spots that never extend to ventral sides. The other segments evenly brownish or with faint patches on the metatarsi that may become annulations on metatarsi III and IV. Male tarsus, metatarsus and part of tibia I with long, rigid, straight hairs (Fig. 21). Terminal apophysis of male palpus without any projecting tooth. The dark sclerotized pieces of the terminal apophysis arranged as in Figures 14, 15. Epigynum as in Figure 25 with the sides of the septum slightly sinuous.

Remarks. The different structure of the terminal apophysis distinguishes the males of *P. purbeckensis, P. mixta* and *P. olympica.* In *P. mixta* and *P. olympica,* the long hairs

covering the first three segments of leg I are longer, more numerous, and are directed forward rather than straight out (compare Fig. 23). It is possible to separate the males of *P. purbeckensis* from those of *P. agrestis*, which has a very similar palp, by the absence of long hairs on the first leg of *P. agrestis*. The different shape of the tegular and terminal apophysis distinguishes *P. purbeckensis* from *P. incerta*, which has a similar arrangement of hairs on the first legs. Hairs are clearly different in *P. plumipes*. The females can be mistaken for those of *P. monticola*, *P. arenicola* (*fucicola* Dahl) and *P. agrestis* (*pseudomonticola* Simon). From *P. monticola*, *P. purbeckensis* is distinguished by the shape of the epigynum, usually featuring a well-marked longitudinal groove extending for about two-thirds of the septum. In contrast, in *P. monticola* the groove is indistinct and very often limited to the anterior half. Also the edges of the anterior pockets are never so divided as in *P. monticola*. *Pardosa purbeckensis* is distinguished from *P. arenicola* by the less sinuous lateral sides of the septum; from *P. agrestis* and *P. incerta* by its much less clearly annulated legs and by differences in annulations of femora. But these characters are so unreliable that very often, as Knülle (1954, p. 72) says: "Die Weibchen von *L. agrestis* und *L. purbeckensis* sind nicht trennbar."

Ecology. Salt marshes seem to be the typical habitat (Knülle, 1954), but it is possible to find *P. purbeckensis* on mud flats near seashores.

Distribution. Great Britain, Denmark, Germany, Netherlands.

Specimens examined came from Germany and England. Illustrations were made from German specimens (Knülle det.).

Pardosa plumipes (Thorell)
Figures 12–13, 22, 32

Lycosa plumipes Thorell, 1875a: 104. Male holotype from Orenburg, southern Russia, in the Natural History Museum, Stockholm, examined;
1875b: 143–144.—Odenwall, 1901: 257–258, figs. 1–4, ♂♀. Strand, 1909: 76–78. [Not *Pardosa plumipes* Mello-Leitão, 1942: 395 (= *Pardosa plumipedata* Roewer).]
Lycosa monticola,—Saito, 1934: 358–359, pl. 15, fig. 87, ♀. Saito, 1959: 53, pl. 5, fig. 302, pl. 6, fig. 306, ♀.
Pardosa plumipes,—Roewer, 1954: 170. Bonnet, 1958: 3407.

Description. Carapace brown. Light median band yellow, narrow, spindle-shaped, tapering anteriorly. Lateral bands yellow, wide. Each lateral band includes, near the margins of carapace, a dark band somewhat as in *P. palustris* (Fig. 16), and much clearer on the female than on the male. Clypeus yellow. The female has yellowish, annulated legs. Metatarsi of fourth pair darker, the annulations tending to merge. Male with light legs. Tibiae and metatarsi of the first pair with long hairs as in Figure 22. (The specimen is in poor condition and the tarsi are lost.) The male palpus, as in Figures 12, 13, is similar to that of *P. purbeckensis*; the epigynum is illustrated by Figure 32.

Remarks. The males of *P. plumipes* can be separated from males of *P. purbeckensis* by the different arrangement of hairs on the first pair of legs. *Pardosa incerta* has a longer and sharper tegular apophysis than has *P. plumipes*. There are also small differences in the terminal apophysis. *Pardosa plumipes* can be separated from *P. mixta* and *P. olympica* by the arrangement of hairs on the first legs. Females differ from those of *P. purbeckensis* in having lateral bands on the carapace much broader and enclosing a dark one. *Pardosa purbeckensis*, in contrast, has the dark lateral bands marginal. The posterior angles of the genital plate of *P. plumipes* project laterally more than in *P. incerta*. Having examined only two females, I cannot make comparisons with the other species.

The two female specimens I examined from Japan were determined by Strand (1909). The carapace pattern agrees very well with that of the male holotype of *P.*

plumipes. The shape of the epigynum agrees with the drawing and description of Odenwall (1901). Unfortunately, the numerous specimens of both sexes studied by Odenwall are lost. *Pardosa monticola,* illustrated by Saito (1934, 1959), must, I think, be regarded as *P. plumipes* (see above); it is certainly not *P. monticola.*

Distribution. Russia: Siberia. Japan: Nemura-Yesso (Strand, 1909); Akkeshi (Saito, 1934, 1959).

Specimens examined came from Orenburg, southern Russia and Nemura-Yesso, Japan.

Pardosa mixta (Kulczynski)
Figure 23

Lycosa mixta Kulczynski, 1887: 299–302, pl. 5, figs. 11, 12, ♂ ♀. Syntypes from Schlern Berg, southern Tyrol, [M. Sciliar, Trentino-Alto-Adige], probably in the Budapest Museum. Kulczynski, 1909: 441–444, pl. 22, fig. 15, ♂. Kratochvil, 1935: 14–16, figs. 2–4, 10, ♂ ♀.
Pardosa mixta,—Roewer, 1954: 167. Bonnet, 1958: 3388. Tongiorgi, 1965: figs. 80–81, 93, 104–105, ♀ ♂.

Description. Carapace brown. Median band pointed in front, in the male often faint anteriorly. Lateral bands continuous, about as broad as the median one, separated from the carapace margins by a narrow dark band, then by another thin light band (fig. 93). In the female the lateral bands extend to the clypeus; in the male the sides of the head are darkened. Legs yellow-brown. Femora with dorsal longitudinal dark marks; the other segments with indistinct rings, clearer on posterior legs. Tarsus, metatarsus, and part of tibia of male with very long lateral and forwardly directed hairs (Fig. 23). Abdomen brown-red. Male palpus with terminal apophysis as in figures 104, 105. Epigynum as in figures 80, 81. Septum a little broader than long. Posterior angles more or less blunt, wrinkled, and sometimes prominent.

Remarks. The male can be mistaken only for *P. olympica* because of the long hairs

on the first three segments of the first pair of legs, but it is distinguished by the terminal apophysis. *Pardosa mixta* can be distinguished from *P. purbeckensis, P. plumipes,* and *P. incerta* by a different arrangement of hair on the legs and by the different shape of the terminal apophysis (see Figs. 21, 22). The females are distinct from *P. blanda* (and *albata*?) and *P. palustris* by the shape of the edge of the anterior pockets. The females of *P. mixta, P. agricola,* and *P. torrentum* differ by the carapace pattern; *P. mixta* differs from *P. monticola* by having the septum broader than long (in *P. monticola* it is longer than broad or as long as broad). Habitat and differences in genital plate distinguish this species from *P. arenicola* and *P. purbeckensis.* The lateral light bands are generally a little broader than the median bands in *P. agrestis* (*pseudomonticola* Simon) while they are about equal in *P. mixta. Pardosa mixta* and *P. olympica* have different septa.

Ecology. *P. mixta* lives on the mountains. In the Alps it seems to prefer altitudes of 2000–2500 m.

Distribution. Switzerland, Italy, Tyrol, Carpathians, Yugoslavia.

Specimens examined came from Switzerland, Italy, and Tyrol. Illustrations were made from Swiss and Italian specimens.

Pardosa olympica n. sp.
Figures 8–9, 17, 30

Type. Male holotype from Attika Moni Pentelli [Mone Pendéli east of Athens], Greece, May 1926 (C. F. Roewer), in the Senckenberg Museum, Frankfurt.

Description. Female. Total length 5.0 mm. Carapace 2.5 mm long, 1.95 mm wide. Carapace brown. Median light band spindle-shaped, reddish yellow; there is a transverse enlargement just behind the posterior eyes as in Figure 17. Lateral bands reddish, narrow, continuous; separated from carapace margins by a dark streak and then by a light, scantily marked one; carapace also with a black marginal line. Clypeus

yellow. Chelicera reddish yellow, a little darkened at the apex. Sternum black, brighter in the middle. Abdomen blackish with the usual reddish pattern of the species of the group. Legs yellow with brown rings. Femora with dorsal rings, almost uniformly brownish color. Metatarsi more or less annulated but with a wide distal ring that sometimes reaches the middle of the segment. Epigynum as in Figure 30. Male. Carapace pattern as in the female. Median light band narrow and tapering anteriorly. Legs yellow. Femora dorsally blotched and slightly darkened ventrally. The other segments are uniform in color. Tarsi, metatarsi, and tibiae of first pair have long white hairs appressed against the segments and directed distally, almost as in *P. mixta* (Fig. 23). The femur of the male palpus is yellow and slightly darkened, patella and tibia are yellow, tarsus is brown. Leg measurements in mm. Female: Femur I, 2.0; II, 2.0; III, 1.9; IV, 2.5. Patella and tibia I, 2.4; II, 2.2; III, 2.2; IV, 3.4. Metatarsus I, 1.5; II, 1.6; III, 2.0; IV, 3.3. Total length leg I, 7.0; II, 6.8; III, 7.0; IV, 10.5. Male: Femur I, 1.8; II, 1.7; III, 1.6; IV, 2.1. Patella and tibia I, 2.3; II, 2.0; III, 2.0; IV, 2.7. Metatarsus I, 1.5; II, 1.5; III, 1.6; IV, 2.7. Total length leg I, 6.6; II, 6.2; III, 6.2; IV, 8.9.

Remarks. Pardosa olympica is closely related to *P. mixta* as shown by the carapace pattern and the structure of the genitalia of the male. The *P. olympica* male differs from *P. mixta* in the structure of the terminal apophysis and the more closely appressed hairs of the first legs. The female differs in the shape of the septum. The posterior angles of the septum are as in *P. mixta* but much more blunt and the edges of the anterior pockets are much more medially bent (Fig. 30).

Considering the similarities of the taxonomic characters among different species of the group it appears that the specimens represent a distinct species rather than a subspecies of *P. mixta*.

Distribution. Greece. Attika: Moni Pentelli

(Roewer), 1 ♂ holotype (SMF, R II/3928), 2 ♀ ♀ paratypes (SMF, R II/14014). *Crete*: plains near Akrotiri Khersónisos (Roewer), 1 ♂ paratype (SMF, R II/3933), May 1926.

Pardosa palustris (Linnaeus)
Figure 16

Aranea palustris Linnaeus, 1758: 623. Type from Sweden, presumably lost.

Lycosa palustris,—Kulczynski, 1887, pl. 5, figs. 9, 10, ♂. Chyzer and Kulczynski, 1891, pl. 2, fig. 13, ♀. Smith, 1907, pl. 2, figs. 6a, b, 7a, b, pl. 4, figs. C, D, E, ♂ ♀.

Lycosa herbigrada,—Holm, 1947, fig. 12b, pl. 5, figs. 52, 53, pl. 10, fig. 28, ♂ ♀. Knülle, 1954, pl. 22, fig. 1, ♂.

Lycosa tarsalis,—Kulczynski, 1909, pl. 22, fig. 9, ♂. Dahl and Dahl, 1927: 47–48, figs. 124–126, ♂ ♀. Kratochvil, 1935: 17, fig. 5, ♂. Palmgren, 1939, figs. 56, 69, 84, ♂ ♀. Locket and Millidge, 1951: 259–261, figs. 123 E, F, 124 D, 126 C, D, 127 F, ♂ ♀.

Pardosa tarsalis,—Simon, 1937, figs. 1648, 1666, 1669, ♂ ♀. Tambs-Lyche, 1940: 16, fig. 1, ♀.

Pardosa andersoni Gertsch, 1934: 16–17. Female holotype from Flaxman's Isl., Alaska, in the American Museum of Natural History. Gertsch and Wallace, 1935, fig. 10, ♀.

Pardosa palustris,—Roewer, 1954: 177. Bonnet, 1958: 3402. Wiebes, 1959, figs. 66–67, ♂ ♀. Tongiorgi, 1966, figs. 84–85, 91, 102–103, ♀ ♂.

Description. In this species occur two essentially different carapace patterns. The typical specimens have a pattern similar to that of *P. monticola.* In several specimens the light lateral bands are separated from the carapace margins by a continuous dark band, but specimens can be found in which the outer dark bands are reduced (fig. 91). These specimens have an abdominal pattern like that of *P. monticola.* Figure 16 represents another form of *P. palustris,* often described as a separate species under the name *P. herbigrada* (Blackwall). The two forms, according to Locket and Millidge (1951, p. 261), often exist in the same population, and are interbreeding. The abdomen of *P. palustris* (*herbigrada*) is usually lighter and the sides of the posterior region are clothed with white hairs. Legs

yellow with more or less distinct annula-
tions. Femora with dark blotches dorsally.
Terminal apophysis of the male palpus is a
broad, slightly curved, more or less sharp
and jagged lamina; it is very characteristic
and unique to this species (figs. 102, 103).
Epigynum as in figures 84, 85. Septum
much broader than long, posterior angles
obtuse, often prominent and wrinkled. A
deep groove extends about two-thirds of the
septum's length. Edge of the anterior
pockets is characteristic. Color variable:
posterior angles generally dark brown-red,
but plate usually evenly colored, or only
one side darkened. Because of the great
variability of the epigynum, I have drawn
only two examples. Tambs-Lyche's (1940)
series of variant silhouettes of the plate
agrees, I find, with the variation in several
populations of *P. palustris* collected in the
Alps.

Remarks. The peculiar structure of the
terminal apophysis of the palpus distin-
guishes the males of *P. palustris* from those
of the other species. The females cannot
be mistaken for any other species, as the
shape of the epigynum is very characteristic,
and though it may vary greatly, it always
permits reliable diagnosis. The edge of the
anterior pockets has the same structure only
in *P. blanda* (and *P. albata?*). The only
closely related species is *P. mixta*, which
often has posterior angles of the septum
similarly wrinkled and prominent, but is
distinguished from *P. palustris* by the edges
of the anterior pockets and by having the
sides of the plate generally more parallel.

Ecology. The species is widespread,
especially in cold climates. It lives on
mountains as well as plains, mostly in open
and rather dry places, meadows, pastures,
and heaths (Knülle, 1954: 71; Holm, 1950).

Specimens examined came from Alaska,
England, France, Germany, Italy, Austria,
Iceland, Denmark, Switzerland. Illustrations
were made from Italian and English spec-
imens.

Distribution. Palearctic to Alaska. *Pardosa*

andersoni from Alaska is *P. palustris* (Fox,
1937: 114).

Pardosa consimilis Nosek
Figures 19, 31

Pardosa consimilis Nosek, 1905: 140–141, pl. 5,
  fig. 18, ♀. Female holotype from Erdschias area
  (Erdjies), Asia Minor, in the Naturhistorisches
  Museum, Vienna, examined.—Roewer, 1954:
  161. Bonnet, 1958: 3364.

Description. Carapace dark brown. Light
median band yellow, oval, scantily branched
on the thoracic region, brownish yellow on
the cephalic region (Fig. 19). Lateral
bands yellow, narrow, continuous, a little
sinuous. Near the carapace margin there
is a very narrow light band covered with
white hairs. White hairs cover the median
and lateral bands also. Abdomen yellow-
red with the usual pattern of the group.
Legs reddish. Femora annulated on upper
sides, more or less uniformly darkened on
the ventral sides. Tibiae and metatarsi
blotched or faintly annulated. Epigynum
as in Figure 31.

Remarks. Since I could examine only the
holotype of this species I cannot make any
comparison with the other species of the
P. monticola group. Nosek compared this
species with *P. blanda* and *P. albata,* but
his opinion appears to be incorrect for both
the septum and the carapace pattern. How-
ever, since the septum is different from
that of other species, it is better to consider
it as a distinct species.

Pardosa arenicola (O.P.-Cambridge)
Figures 6–7, 18

Lycosa arenicola O.P.-Cambridge, 1875: 253–
  255, pl. 8, figs. 9a, b, ♀ ♂. Female and male
  syntypes from Island of Portland, Chesil Beach,
  England, in the University Museum, Oxford.
  Smith, 1907, figs. 1a, b, ♀ ♂. Kulczynski, 1909,
  pl. 22, fig. 10, ♂. Dahl and Dahl, 1927: 52,
  figs. 136–138, ♀ ♂. Locket and Millidge, 1951:
  252–255, figs. 123 A, 124 A, B, ♂ (sub. *L.
  agrestis* and *L. purbeckensis;* see Wiebes, 1959:
  41), 125 A, B, ♂, 127 A, ♂ ♀. Knülle, 1954,
  pl. 22, fig. 2, ♂.

Pardosa arenicola,—Simon, 1937, figs. 1630, 1671, ♂ ♀. Roewer, 1954: 159. Bonnet, 1958: 3357. Tongiorgi, 1966, figs. 75–76, ♀.

Description. Carapace dark brown. Median light band narrow and anteriorly pointed. Lateral bands broken into three parts by three thin dark lines (Fig. 18). The lateral spots may be well separated or so close as to form a continuous band in what Dahl (1908) called *P. arenicola fucicola.* Legs yellow-brown. Femora with dorsal dark blotches. Sometimes uniformly darkened or inconspicuously annulated. Metatarsi and tibiae with more or less distinct annulations on the tips. Abdomen brown-red. Abdominal pattern not distinct and about the same color as the background. Terminal apophysis of male palpus bicuspid. Tegular apophysis very long and narrow, sharpened at the end (Figs. 6–7). Epigynum as in figures 75, 76. Septum with sides strongly sinuous, very often lobed at the posterior third, about as long as broad, and entire length grooved.

Remarks. The male is easily distinguished by the presence of two teeth on the terminal apophysis. From *P. agricola,* which also has two teeth on the terminal apophysis, *P. arenicola* may be distinguished by the different shape of the tegular apophysis and by the carapace pattern. The females can be distinguished by the carapace pattern. If this is insufficient, e.g., *P. arenicola* (*fucicola*), the following characters may be used: unlike *P. agricola* and *torrentum*, *P. arenicola* has the legs slightly or not at all annulated; unlike *P. agrestis,* *P. arenicola* has the lateral sides of the septum strongly sinuous and almost as wide as long; unlike *P. agrestis* (*pseudomonticola* Simon) and *P. purbeckensis,* *P. arenicola* (*fucicola*) has the leg color almost uniform and the median and lateral bands often obscure. If all these characters fail, distinguishing among these species may be very difficult.

Lehtinen and Kleemola (1962) and also Locket (1964) doubt the validity of this species. They consider *P. arenicola* as an ecological form of *P. agricola.*

Ecology. *Pardosa arenicola* lives on sand and pebble beach near the sea. (For further information about the habitat of this species see Knülle, 1954.)

Specimens examined came from England (MCZ) and Germany (coll. and det. by Knülle). Illustrations were made from English specimens.

Distribution. Great Britain, France, Germany, Denmark, Finland, Sweden, Poland, Switzerland, Czechoslovakia, Italy (Di Caporiacco, 1940, 1950). *Pardosa arenicola* does not appear to go south of 48° latitude. The Italian records of Di Caporiacco were based on some specimens found on Cima Galbana (1583 m, Monti Lessini, Veneto) and are therefore very doubtful, and on one female collected on a sand bank of Laguna of Venice.

Pardosa agricola (Thorell)

Lycosa arenaria C. L. Koch, 1834: 123, pls. 15, 16, ♀ ♂. Syntypes from the Danube bank near Regensburg, Germany, probably in the British Museum, London. [Not *L. arenaria* Savigny and Audouin, 1825].
Lycosa agricola Thorell, 1856: 171. New name for *L. arenaria* C. L. Koch. Smith, 1907, pl. 1, figs. 2a, b, ♀ ♂. Dahl and Dahl, 1927: 53, figs. 139–141, ♀ ♂. Kratochvil, 1935: 17, fig. 7, ♂. Holm, 1947: 26, fig. 13c, pl. 5, figs. 50–51, pl. 10, figs. 31–32, ♂ ♀. Locket and Millidge, 1951: 255, figs. 123 B, 124 A, B, ♂ (under the erroneous name of *L. agrestis* and *purbeckensis*), 125 C, D, 127 b, ♂ ♀.
Pardosa agricola,—Simon, 1937, figs. 1631, 1632, 1662, ♂ ♀. Roewer, 1954: 157. Bonnet, 1958: 3348. Tongiorgi, 1966, figs. 77–79, 98, 107–108, ♀ ♂.

Description. Carapace dark brown. Light median band dilated anteriorly, sometimes branched on the thoracic region (fig. 98). On several specimens the median band is not broader than the lateral ones, and on some the anterior enlargement is not clearly evident. Lateral bands clearly broken. Occasionally the posterior spots merge. Ab-

domen very dark with brown-red pattern. Legs yellow, very distinctly annulated. Male palpus with two teeth on the terminal apophysis. Tegular apophysis long and blunt at the end (figs. 107, 108). The female genital plate is about as long as broad. Lateral sides very sinuous. Edge of the anterior pockets as in figures 77–79. (Owing to the great variability, *P. agricola* can often be mistaken for *P. agrestis, P. torrentum* or *P. arenicola.*)

Remarks. The male is easily distinguished from the other species by the two-toothed terminal apophysis. The tegular apophysis, clearly blunt at the end, is a good character for separating *P. agricola* from *P. arenicola*, which has a long and tapering apophysis (compare Figs. 6, 7).

The females can be confused with *P. torrentum, P. agrestis (pseudoagricola* Dahl), and sometimes with *P. arenicola*; however, the carapace pattern distinguishes *P. agricola* from all others. *Pardosa arenicola* has a different carapace pattern (Fig. 18) and much less distinct annulations on the legs.

The genital plate of *P. agrestis* and of *P. torrentum* is broader than long, while that of *P. agricola* is generally as long as broad.

The lateral sides of the septum are very sinuous. The edges of the anterior pockets are useful in distinguishing the species from *P. agrestis*. The abdominal pattern can be used when distinguishing between *P. agricola* and *P. torrentum*: *torrentum* generally has a yellow or yellow-red abdominal pattern, and it is always lighter than *P. agricola*.

A good ecological and taxonomic diagnosis of this species has been given by Lehtinen and Kleemola (1962) for Finnish specimens. They also supplied illustrations of the ventral and dorsal views of the epigynum.

Ecology. According to Dahl and Dahl (1927: 52, 53), and Locket and Millidge (1951: 255), *P. agricola* prefers open, sandy or stony banks of lakes and water courses. It does not seem to reach high altitudes. (See also Knülle, 1954: 73.)

Specimens examined came from Finland, Munkki near Simo (Papi leg.), England (MCZ). Illustrations were made from Finnish and English specimens.

Distribution. Europe, Siberia, Asia, Iran (Roewer, 1955). Roewer (1954: 157) indicates that *P. agricola* is a central and northern European species, but this species has also been found by Roewer (1959) in Greece, Crete, and Anatolia. It is probable that it has often been mistaken for *P. torrentum*. At least *Pardosa agricola* seems more common in northern than in southern Europe.

Pardosa torrentum Simon

Pardosa torrentum Simon, 1876: 313–314, pl. 13, fig. 26, ♀. Male and female syntypes from Lautaret, Briançon, in the Muséum National d'Histoire Naturelle, Paris. Simon, 1937, figs. 1641, 1664, ♂ ♀. Roewer, 1954: 174. Bonnet, 1958: 3426. Tongiorgi, 1966, figs. 86, 87, 99, 109, 110, ♀ ♂.

Lycosa torrentum,—Kulczynski, 1909, pl. 22, fig. 13, ♂. De Lessert, 1910: 507–508.

Description. Carapace dark brown. Some specimens collected on the plain near Pisa and near Barletta, Italy, are lighter yellow-brown (compare Chyzer and Kulczynski, 1897: 297). Median band wide, dilated anteriorly, sometimes branched in the thoracic region (fig. 99). Lateral bands broken into three or four spots, not always as light as the median band, and often very faint in the males. Frequently the two posterior spots blend; sometimes all spots are so close as to form a continuous band (var. *integra* Denis, 1950: 106). Legs yellow-brown. Femora with dorsal brown marks, the other segments (except tarsi) annulated. Annulations always distinct but less so than in *P. agricola.*

Abdomen dark brown, almost black. Anterior median stripe brownish, bordered anteriorly with black, flanked and followed by bright yellow-red pattern. The light spots generally surrounded by a purplish or black area. Femur and patella of male palpus clothed with white hairs. Tegular

and terminal apophyses as in figures 109, 110. Epigynum as in figures 86, 87. Septum broader than long, rarely as broad as long.

Remarks. The male is distinguished from *P. agricola* and *P. agrestis* (*pseudoagricola* Dahl) by the different shape of the terminal apophysis and from all other species by the carapace markings. It is very difficult to separate the females of *P. torrentum* from those of *P. agricola* and *P. agrestis.* The abdominal pattern is lighter in *P. torrentum,* while in both other species the pattern is generally brown-red with little contrast against the background. The legs of *P. agricola* are clearly annulated, less clearly so in *P. torrentum,* and often only slightly annulated in *P. agrestis.*

The septum is usually broader than long in *P. torrentum* and *P. agrestis,* and as long as broad in *P. agricola.* The carapace markings set this species apart from the remaining species of the *monticola* group.

Ecology. This species lives in the mountains as well as on the plains. I found some specimens in Italy in areas near the sea. Denis (1950, 1952, 1955) found specimens several times in the Pyrenees between 1000 m and 2500 m. De Lessert (1910) reported that this species lives in the plains as well as in subalpine regions. It seems to prefer open sandy places with scant vegetation or meadows near streams and rivers.

In Italy this species seems more common than *P. agricola,* that is, without taking into consideration that many citations of this species are probably *P. torrentum.*

Specimens examined came from Italy and Tyrol (MCZ). Illustrations were made from Italian specimens collected near Pisa (Toscana), and Casale Monferrato (Piemonte) (MSNG).

Distribution. France, Switzerland, Tyrol, Italy, Hungary, Pyrenees.

Pardosa agrestis (Westring)

Lycosa agrestis Westring, 1861: 480. Female holotype from Sweden. Bösenberg, 1902, pl. 35, fig. 547, ♂ ♀. Smith, 1907, pl. 1, fig. 3, ♂. Dahl and Dahl, 1927: 50, figs. 130–132, ♂ ♀. Kratochvil, 1935: 17, fig. 12, ♂. Holm, 1947: 26, fig. 13b, pl. 10, fig. 30, ♂ ♀. Locket and Millidge, 1951: 255–258, figs. 123, 126 A, B, 127 C, ♂ ♀. Knülle, 1954, pl. 22, figs. 4a, b, c, 6, ♂.

Pardosa agrestis,—de Lessert, 1910: 509, figs. 222–224. Simon, 1937, figs. 1628, 1629, 1665, ♂ ♀. Roewer, 1954: 156. Bonnet, 1958: 3346. Tongiorgi, 1966, figs. 72–74, 95–97, 100–101, ♀ ♂.

Description. Carapace dark brown. Median and lateral bands are highly variable, but three principal types are found: one has the median band anteriorly dilated and the lateral bands continuous (fig. 95); another type has the median band anteriorly dilated but the lateral bands broken (*pseudoagricola* Dahl) (fig. 97); the third type has the median band pointed in front and the lateral bands continuous (*pseudomonticola* Simon) (fig. 96). One or another of the three types may be found alone or most frequently in one population (compare Knülle, 1954: 75; de Lessert, 1910: 509, note). Legs light. Annulations more or less clear. The dark marks on dorsal side of femora may reach to ventral side (compare *P. purbeckensis*). Terminal apophysis of male palpus without any projecting tooth (figs. 100, 101). Epigynum highly variable. Septum broader than long. Edge of the anterior pockets generally as in figures 72–74.

Remarks. The lack of projecting teeth on the terminal apophysis makes the males of this species very close to those of *P. purbeckensis, P. plumipes,* and *P. incerta.* However, they can be distinguished by the length of the hairs on the legs: longer on the first pair of legs of *P. purbeckensis, P. plumipes,* and *P. incerta,* but of the same length on all four pairs in *P. agrestis.* The females are easily distinguished by the carapace pattern when as in figure 95; otherwise they are very hard to identify. *Pardosa agrestis* with the median band anteriorly pointed and continuous lateral bands

is distinguished from *P. blanda* and *P. palustris* by the different shape of the edge of the anterior pockets (compare figs. 84, 85, 88, 89); from *P. mixta* by having the lateral bands a little broader (perhaps) than the median one, and also the epigyna of the two species are different (compare figs. 80, 81). *Pardosa monticola* has the septum at least as long as broad while *Pardosa agrestis* has the septum broader than long (see fig. 83). *Pardosa agrestis* has the lateral sides of the plate less sinuous and has a different ratio of length to width than has *P. arenicola* (compare figs. 75, 76). Differences in annulation of the legs and in the marking of the femora have been found in *P. agrestis*, *P. incerta*, and *P. purbeckensis*. *P. agrestis* and *P. incerta* are much alike. Sometimes *P. agrestis* has a plate much like that of *P. pontica* (compare Fig. 24 and fig. 73). The specimens having the carapace pattern as in figure 97 resemble *P. agricola* and *P. torrentum*. *Pardosa agricola* has the septum about as long as broad with lateral sides generally more sinuous. The legs, moreover, are very distinctly annulated. The lighter abdominal pattern of *P. torrentum* seems to be the best character for distinguishing this species from *P. agrestis*.

Ecology. According to several authors this species lives in the mountains above 2000 m as well as on the plain or near the sea. *Pardosa agrestis* seems to prefer open dry places or fields.

Specimens examined came from France, Austria, England, Italy, Finland, Germany. Illustrations were made from Italian and Finnish specimens, also from French and English specimens (MCZ).

Distribution. Europe, Turkestan, Siberia, Asia. Schenkel (1936: 238) records the presence of *P. agrestis* (1 ♂) in China. He refers to the lateral apophysis of this specimen: "2 kleine dornformige, divergierende Zähne des Vorderrandes liegen tief in der Laminamulde und sind darum schwer zu sehen." Among the species of the *P. monticola* group that I know, only *P. agricola* and *P. arenicola* have two teeth on the terminal

apophysis. Thus the Schenkel specimens cannot be *P. agrestis*.

Pardosa monticola (Clerck)

Araneus monticola Clerck, 1757: 91, pl. 4, fig. 5, ♂ ♀. Syntypes from Sweden, probably lost.
Lycosa monticola,—Bösenberg, 1902, pl. 35, fig. 549, ♂ ♀. Smith, 1907, pl. 1, figs. 4a, b, pl. 4, fig. A, ♂ ♀. Kulczynski, 1909, pl. 12, fig. 17, ♂. Dahl and Dahl, 1927: 49, figs. 127–129, ♂ ♀. Kratochvil, 1935: 17, fig. 11, ♂. Holm, 1947: 26, fig. 13a, pl. 10, fig. 29, ♂ ♀. Locket and Millidge, 1951: 259, figs. 123 G, 124 C, 126 E, F, 127 E, ♀ ♂. Knülle, 1954, pl. 22, figs. 3a, b, ♂.
Pardosa monticola,—F. P.-Cambridge, 1895, pl. 4, figs. 5, 7c, 8c, 11, ♂ ♀. Simon, 1937, figs. 1658, 1672, ♂ ♀. Wiebes, 1959, figs. 59, 70, ♂ ♀. Roewer, 1954: 167. Bonnet, 1958: 3390. Tongiorgi, 1966, figs. 83, 94, 111, 112, ♀ ♂.

Description. Carapace brown. Median light band pointed anteriorly. Lateral bands continuous and extending to the clypeus (fig. 94). Sides of the head sometimes darkened. Lateral bands slightly broader than the median one. Lateral bands separated from carapace margins by a single dark streak (compare *P. mixta*, fig. 93). Legs light yellow, spotted on upper side, often annulated, especially tibiae and metatarsi three and four. Terminal apophysis with a little tooth (figs. 111, 112), distinctly shorter than in *P. blanda*, *P. albata*, and *P. torrentum*. Tegular apophysis long and rather sharp. Palpus clothed with black hairs only. Epigynum as in figure 83. Septum generally longer than broad (but sometimes as long as broad). Median groove limited to the anterior half. The posterior part of the septum raised slightly in the middle.

Remarks. The male of *P. monticola* is distinguished from those of *P. blanda*, *P. albata*, and *P. torrentum* by the absence of white hairs on the palpus. From *P. torrentum* it also differs by the carapace pattern. From all the other species it differs in the shape of the terminal apophysis. The female of *P. monticola* differs from those

of *P. palustris* and *P. blanda* (and probably *P. albata*) by having the septum at least as long as broad. *Pardosa monticola* differs from *P. mixta* in carapace pattern and by having the posterior angles of the plate less blunt and wrinkled (compare figs 80, 81). It differs very little from *P. purbeckensis* and *P. agrestis* (*pseudomonticola* Simon). It can be distinguished from *P. purbeckensis* by the slightly different shape of the epigynum; specifically, *P. purbeckensis* has the sides of the septum a little more sinuous and the median groove more pronounced. *Pardosa agrestis* has the septum broader than long. From *P. arenicola* (*fucicola* Dahl) it is distinguished by the much smaller size of the septum, and by having the sides of the septum not so sinuous and the median groove not so deep. *Pardosa occidentalis* has a septum resembling that of *P. monticola* but carapace patterns are different. The shape of the plate is useful to distinguish *P. monticola* from the other species.

On Sila Mountain (Calabria, southern Italy) near the shores of Arvo and Cecita lakes (F. Papi, August 1958), and on the slopes of Monte Pollino 1800 m (E. Mayr, May 1957, MCZ), a population of *P. monticola* has been found whose males have the tegular apophysis shorter and not as sharply pointed. Both males and females are slightly smaller. These specimens are probably not *P. monticola minima* Simon (figs. 82, 92, 113, 114).

In my previous paper (Tongiorgi, 1966) a table giving the measurements of twelve female specimens of *P. monticola* from Sila and ten specimens collected in different countries of Europe (Italy, Germany, France, England) are recorded. The drawings of *P. monticola* in Saito (1934, 1959, pl. 5, fig. 30a, pl. 6, fig. 30b) do not agree with this species. It seems to me that the spider represented is too gray and the lateral bands of carapace too broad (about twice the width of the median band). Only a fine broken dark line is visible in the

middle of each band. It is probably *P. plumipes*.

Ecology. This species lives on the mountains as well as on the plains, on the mountain-grassland as well as on dry, open ground heaths near the sea. According to de Lessert (1910: 511) and from my own observations, this species does not seem to reach high elevations in the Alps. Above 2000 m it is replaced by *P. mixta*. (For further information on the ecology of this species see Knülle, 1954, and Wiebes, 1960.)

Specimens examined came from Italy, Germany, Switzerland, France, Ireland, Denmark, England. Illustrations were made from Italian specimens.

Distribution. Europe, Siberia, China, Afghanistan (Roewer, 1960).

Pardosa occidentalis Simon
Figure 28

Pardosa occidentalis Simon, 1881: 135. Female holotype from Portugal, in Muséum National d'Histoire Naturelle, Paris, examined.—Roewer, 1954: 169. Bonnet, 1958: 3398.

Description. Carapace brown with median and lateral bands yellow. Median band slightly broadened anteriorly and at level of the thoracic furrow where it is slightly branched. The two wide areas are about the same width. Lateral bands are continuous, as wide as the median one, serrated on the upper margin, and continuous on clypeus. There is a narrow dark band, barely evident, near the carapace margins. Legs yellow. Femora with dorsal blotches. Epigynum as in Figure 28.

Remarks. The only specimen known of this species is the holotype, here illustrated. It is impossible to judge whether it is a good species or not. Judging by the shape of the epigynum, *P. occidentalis* is closely related to *P. monticola* but the carapace pattern is different. The shape of the epigynum and absence of leg annulations distinguish it from *P. agrestis*.

Pardosa blanda (C.L. Koch)
Figure 27

Lycosa blanda C. L. Koch, 1833: Heft 120, pl. 24, ♂. Male holotype and female paratype from near Nassfelde, Salzburg, Austria, probably in British Museum, London. Kulczynski, 1909, pl. 22, fig. 12, ♂. Kratochvil, 1935: 17, fig. 8, ♂. Dahl and Dahl, 1927: 51, figs. 133–135, ♂ ♀.

Pardosa cursoria,—Simon, 1876: 316–318.

Pardosa blanda,—Simon 1937, figs. 1647, 1670, ♂ ♀. Roewer, 1954: 160. Bonnet, 1958: 3360. Tongiorgi, 1966, figs. 88–90, 115, 116, ♀ ♂.

? *Pardosa subalpina* Schenkel, 1918: 97. Female holotype from Klein Scheidegg bei Wengen, Berner Oberland, Switzerland, in the Naturhistorischen Museum of Basel, examined.

Description. Carapace dark brown. Median light band narrow, spindle-shaped, sometimes a little enlarged at the anterior end and at the level of the median furrow. Here occasionally faintly branched. Median band clothed with white pubescence. A narrow line made up of light pubescence may continue between the posterior median eyes. Lateral bands yellow. Often two very thin dark lines divide each band into three light spots (fig. 90). Lateral bands about as broad as the median one. Between the lateral band and the carapace margin there is a dark brown band narrower than the light one. The lateral bands do not continue forward on the clypeus but stop on the sides of the head.

Abdomen with reddish pattern on almost black background. Ventral side thickly clothed with white pubescence. Legs dark. Femora uniform or with dark brown spots on dorsal side. Tibiae and metatarsi annulated especially on the posterior legs. Distal end of femur and patella of male palpus clothed with white hairs. Terminal apophysis forms a strong tooth as in figures 115, 116. Septum broader than long, not greatly variable in shape. Edge of the anterior pockets as in figures 88, 89.

Remarks. The male is very close to *P. albata, P. pontica, P. monticola,* and *P. torrentum,* especially in the terminal apophysis of the palpus. It is distinguished from *P.*

monticola by the larger terminal apophysis and the thicker tegular apophysis. Further, *P. monticola* does not have white hairs on the palpus. *Pardosa albata* and *P. pontica* have the palpus entirely clothed with white hairs. *Pardosa torrentum* has a different carapace pattern. The females are distinguished from those of *P. monticola* and *P. mixta* by the edge of the anterior pockets (compare figs. 80, 81). *Pardosa blanda* is distinguished from *P. purbeckensis* by having the septum clearly broader than long (*P. purbeckensis* has the plate almost as broad as long), and by the darker legs. It is distinguished from *P. palustris* by the shape of the septum. *Pardosa blanda* is easily distinguished from all other species by the epigynum and the carapace pattern. It may sometimes be difficult to separate *P. blanda* from *P. agrestis* (*pseudomonticola* Simon). The latter has the lateral bands continuous around the head while in *P. blanda* these are often broken off anteriorly on the sides of the head.

I have not been able to examine any female specimens of *P. albata.* Kratochvil (1935) pointed out lighter coloring of the legs and greater length of patella and fourth tibia compared to fourth metatarsus. These characters cannot be used to distinguish *P. blanda* and *P. albata.* I have often found considerable variation in color and length of the leg segments.

Note. Only the female holotype of *Pardosa subalpina* is known. Schenkel described the specimen, and gave it a new name, though in doubt. The general features, the carapace, and abdominal pattern are like *P. blanda.* The epigynum is very different. It is difficult to establish whether this specimen is an abnormal, teratological one of *P. blanda* or actually belongs to a different species. It is my opinion that *P. subalpina* must be considered an anomalous specimen of *P. blanda.* As it is impossible to draw a conclusion from only one specimen, I limit myself to an illustration (Fig. 27).

Ecology. Pardosa blanda lives in mountains between 1000 m and 3000 m, but most

frequently at about 2000 m. *P. albata* also reaches these elevations. As far as I know, the southernmost point recorded for this species is Varco del Monte Pollino (about 2000 m) in the south of Italy (Simon, 1882).

Specimens examined came from Italy (Alps and Appennines), Switzerland, Yugoslavia, and Austria. Illustrations were made from Italian specimens.

Distribution. France, Germany, Switzerland, Italy, Czechoslovakia, Austria, Poland, Hungary.

Pardosa albata (L. Koch)

Lycosa albata L. Koch, 1870: 36–38. Female and male syntypes from the Tatra Mts. and Bucowina, Carpathian Mts., probably in the Berlin Museum.—Kratochvil, 1935: 17, fig. 9, ♂.

L. albatula Roewer, 1951: 438. New name for *P. albata* thought preoccupied by *Tarentula albata* Nicolet.

Pardosops albatula Roewer, 1954: 196.

Pardosa albata,—Bonnet, 1958: 3350. Tongiorgi, 1966, figs. 117, 118, ♂.

Description. I could examine only two specimens of this species in the collection of spiders from Carnia studied by Di Caporiacco (1922, 1927), and preserved at the Museum of Natural History of Florence. The only differences from *P. blanda* are that the palpus is covered with white pubescence from the base of the femur to about the middle of the tarsus, and that the tegular apophysis (figs. 117, 118) has a slightly different shape.

For the females, the only drawings I was able to find (Chyzer and Kulczynski, 1891, pl. 2, fig. 10a, b; Bösenberg, 1902, pl. 35, fig. 550; Kolosvary, 1937: 404, fig. 1) did not portray any difference from *P. blanda,* and the description by Koch and the distinctive characters from *P. blanda* (*L. cursoria* in Koch, 1870: 42) are not sufficient to separate the females of these two species. Two females borrowed from Dr. Balogh (University of Budapest) determined by Chyzer (Chyzer Coll. no. 1187) as *P. albata* seem to be identical with *P.*

blanda. Pardosa pontica is closely related to *P. albata* but does not have white hairs on the tarsus of the male palpus (compare *P. pontica* Figs. 10, 11 and page 352).

Roewer includes *P. albata* (= *L. albatula* Roewer, 1951) among the species of his new genus *Pardosops* (Roewer, 1954: 196), based chiefly on the presence of two teeth on the posterior edge of the chelicerae (Roewer, 1958: 18, 150). I think the character is not acceptable. I found my specimens have three teeth on the posterior edge of the chelicerae and variation in the number of teeth occurs in other species of this genus (i.e. *P. morosa* L. Koch). Besides, I see no reason to split up this very homogeneous group by assigning species to an artificial genus.

Ecology. This species has been found in mountains.

Distribution. Germany, Hungary, Poland, Russia, Siberia, Italy, Carpathians, Balkans, Transylvania.

Pardosa pontica (Thorell)
Figures 10, 11, 24

Lycosa pontica Thorell, 1875: 100. Male lectotype here designated and one female paralectotype from Alma, Bajnklanbatt, Sympheropolin, southern Russia, in the Zoological Museum, Helsinki, examined.

Pardosops pontica,—Roewer, 1954: 197.

Pardosa pontica,—Bonnet, 1958: 3407.

Note. Thorell (1875: 143) writes that he examined two females of this species. Actually one of the two females determined by Thorell does not belong to the *P. monticola* group, but to a species closely related to *Pardosa saltuaria* (L. Koch).

Description. Carapace brown. Light median band spindle-shaped. Lateral bands yellow, continuous. Each lateral band includes near the margins of carapace a dark band. The carapace as well as the rest of the body is covered with white hairs. Clypeus yellow. Legs of the female have blotches on upper sides of femur. Tibiae and metatarsi with very pale annulations. The male has femora blotched only on

upper sides; other segments uniform. Numerous white hairs make the legs of alcoholic specimens appear pale yellow-white. Male palpal segments yellow with brown blotches on femora (Figs. 10, 11). White hairs on all segments except tarsus. Epigynum as in Figure 24.

Remarks. The male of *P. pontica* is distinguished from that of *P. albata* by the lack of white hairs on the palpal tarsus, and by the slightly different pattern on the carapace. I did not see any females of *P. albata*, thus do not know how the two species differ. The female of *P. pontica* is similar to that of *P. agrestis*, at least in the shape of the epigynum (Fig. 24). Illustrations were made from the lectotype and paratype. Concerning the inclusion of *P. pontica* in the genus *Pardosops* (Roewer, 1954), see the comments above under the preceding species *P. albata*.

Distribution. Southern Russia: Cherson Taurica; Alman, Bujuk-Lambat, Symphero-polin, Balkan. I could not consult the work of Drensky (1936) but he could have mistaken *P. pontica* for *P. albata*. This species seems common in the Balkan region.

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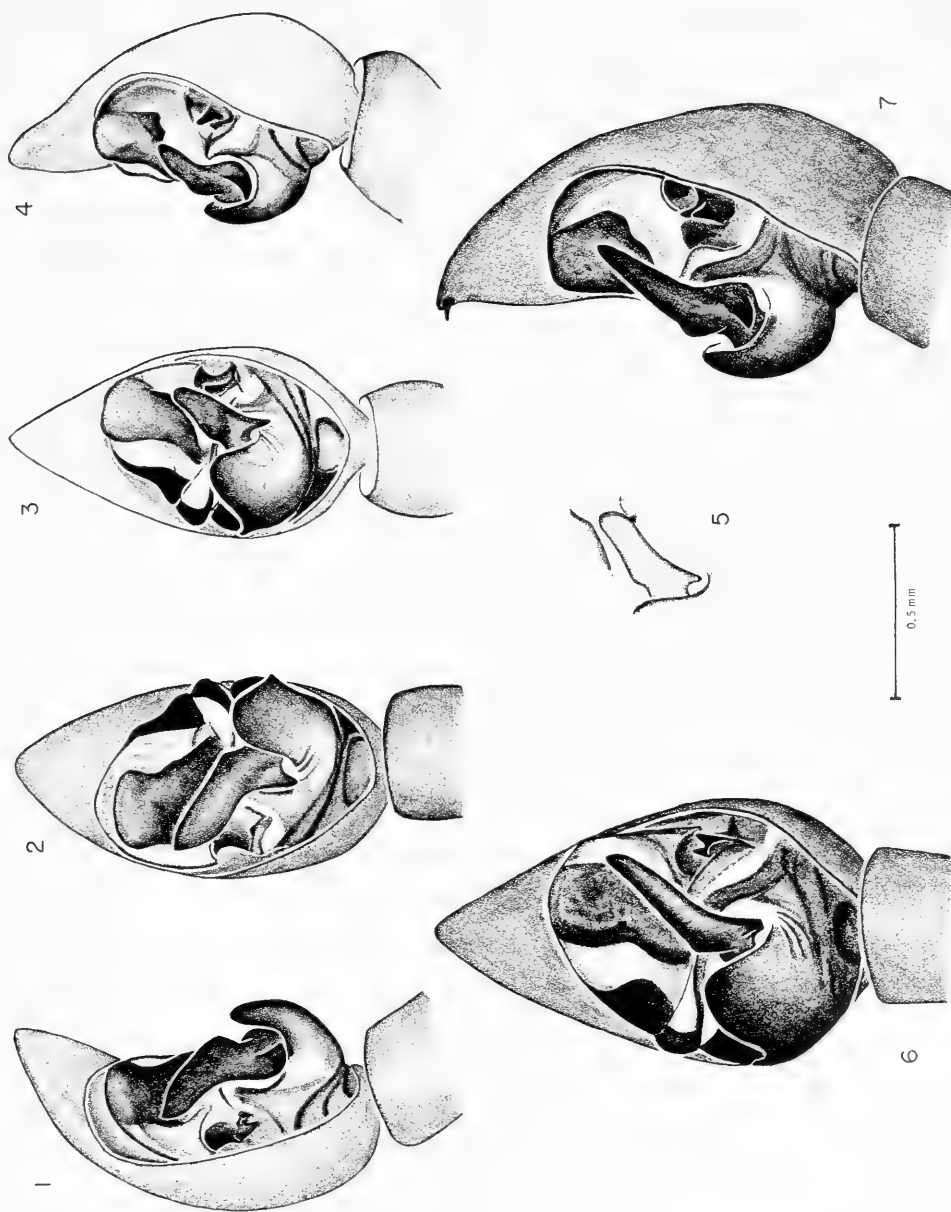
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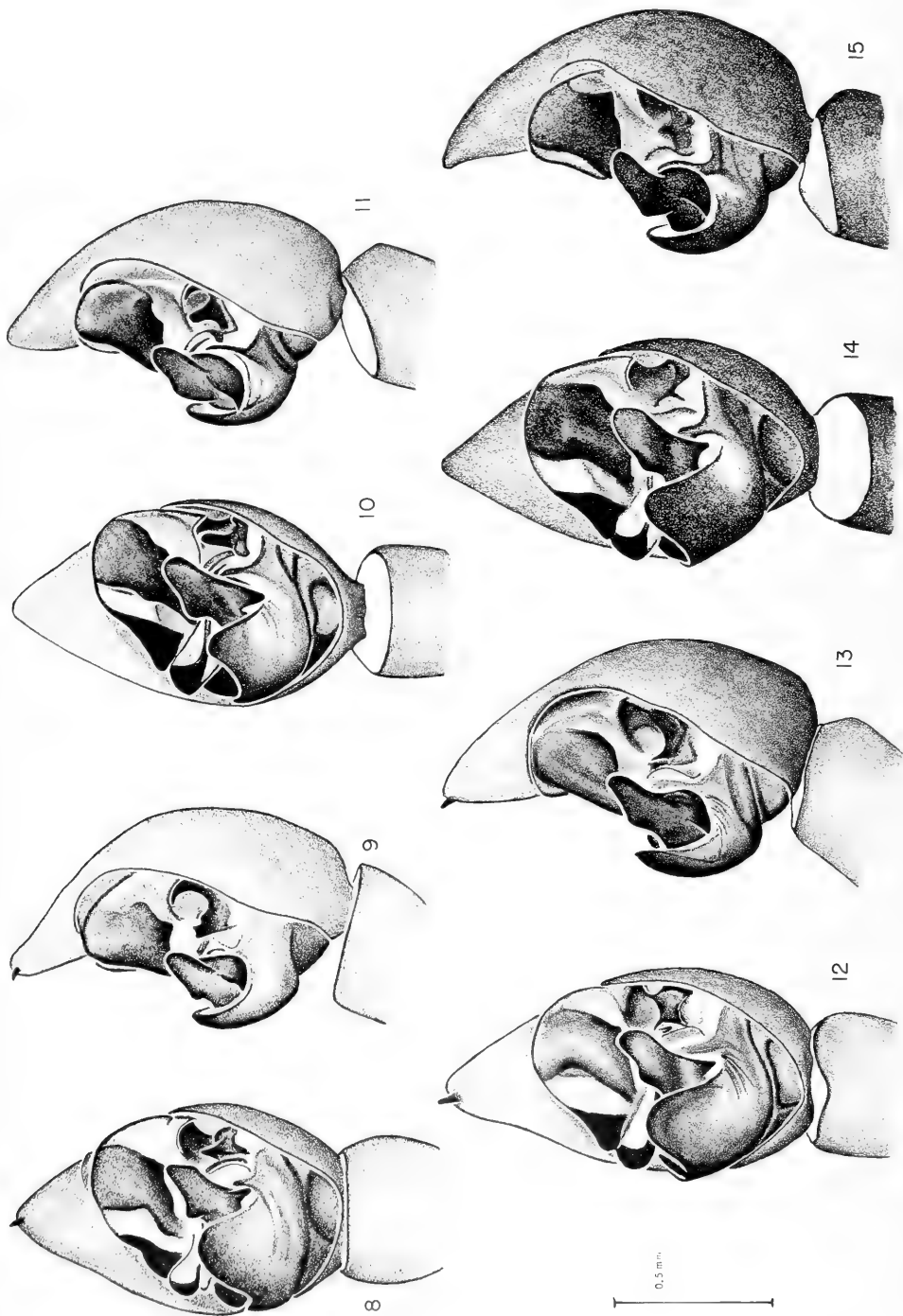
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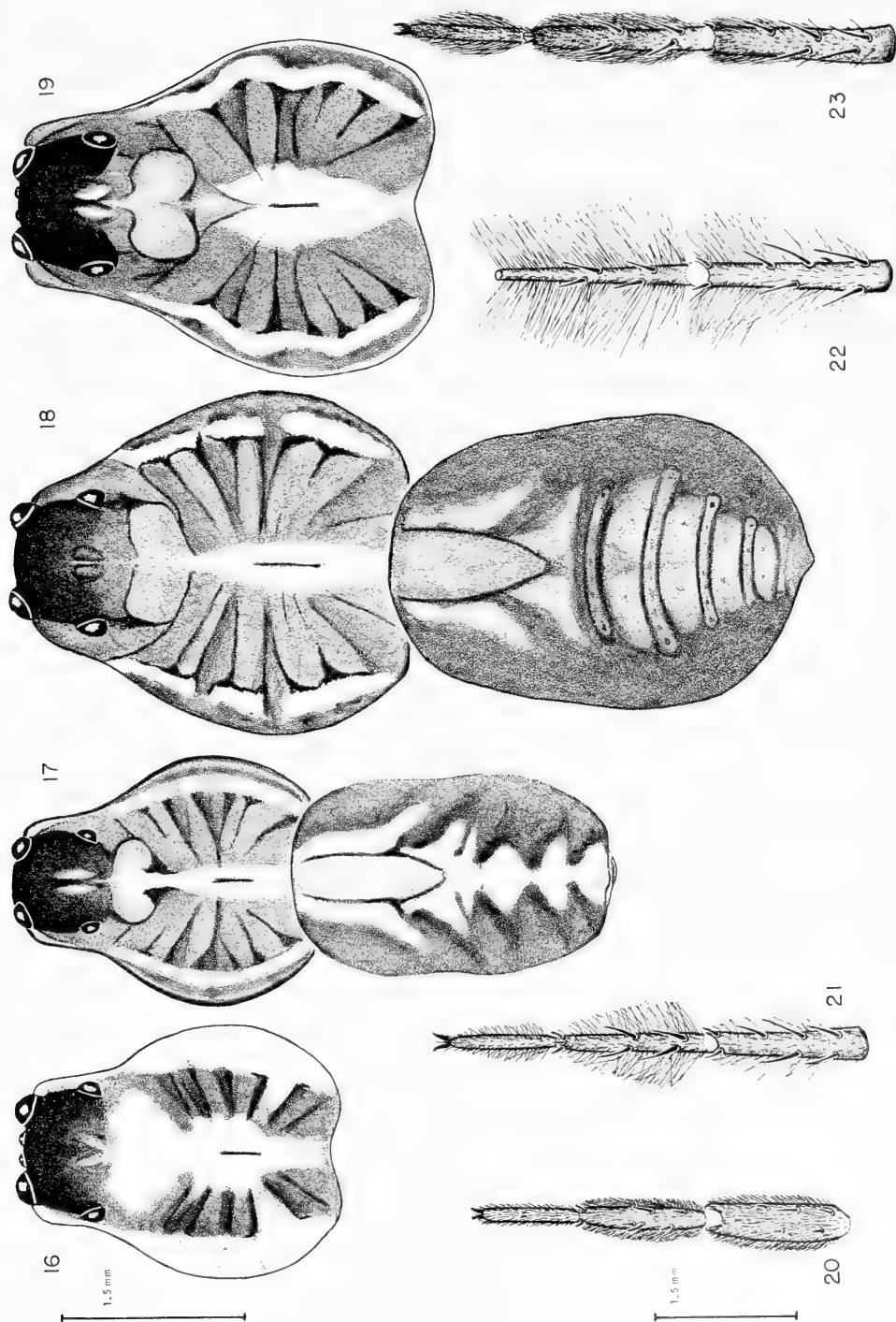
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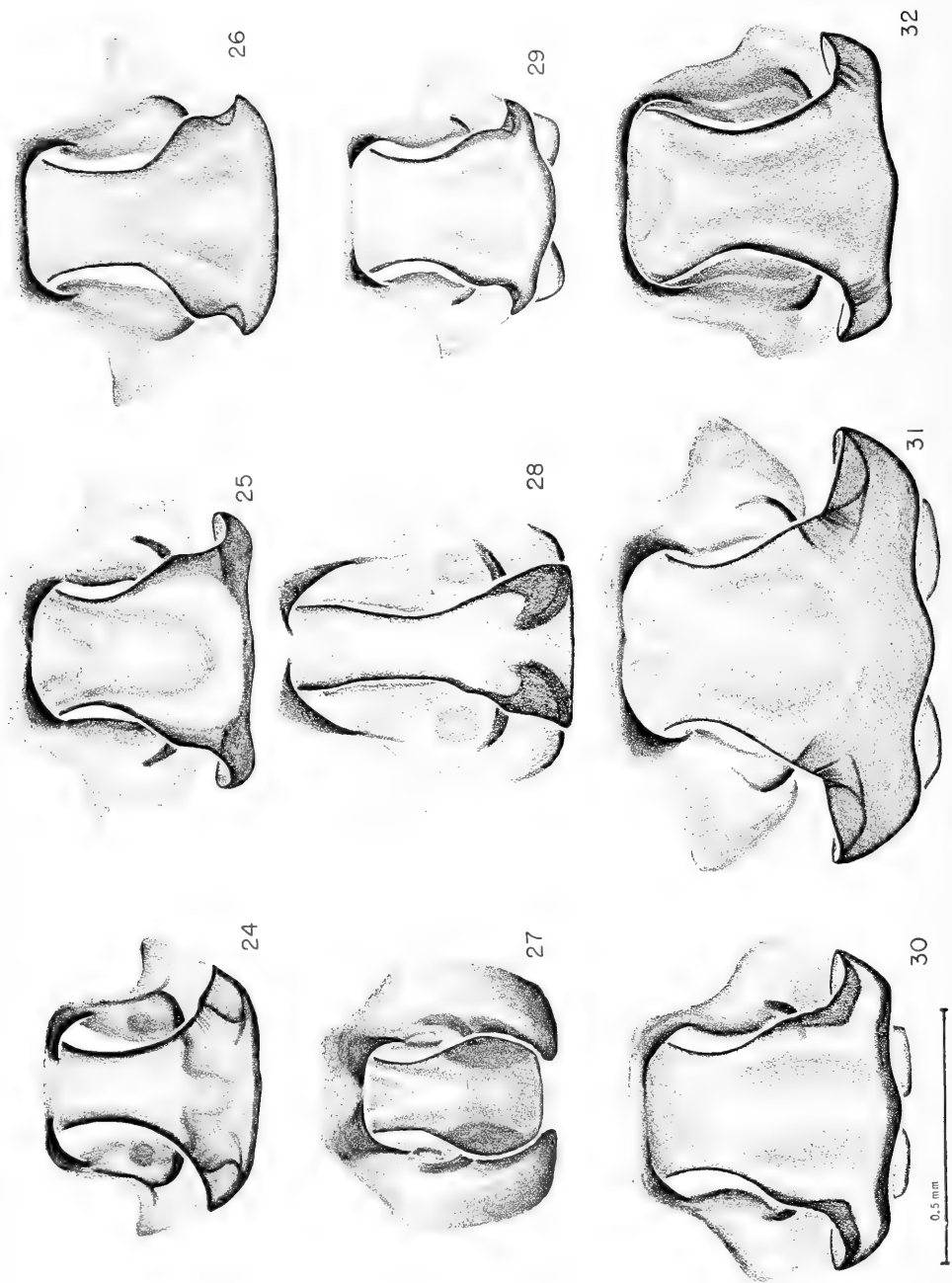
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The Lower Triassic Formations of the Salt Range and Trans-Indus Ranges, West Pakistan

Bernhard Kummel

THE LOWER TRIASSIC FORMATIONS OF THE SALT RANGE AND TRANS-INDUS RANGES, WEST PAKISTAN

BERNHARD KUMMEL

INTRODUCTION

The Triassic formations in the Salt Range of West Pakistan have played a particularly important role in the development of our Triassic zonal scheme, especially for the Scythian stage. In addition, interest in these formations is heightened because they conformably overlie late Permian formations, and the Triassic formations in the Salt Range have occupied the attention of nearly every student of the causes of abrupt faunal breaks. This great interest has not been matched by many modern detailed stratigraphic or paleontologic studies of these Permo-Triassic formations.

Waagen's (1895) great monograph on the "Fossils of the Ceratite Formation" was the first large scale report on a Triassic fauna from the eastern region of Tethys. In the same year Mojsisovics, Waagen, and Diener (1895) published their proposal for a classification of the Triassic System. In that paper the name Scythian was introduced for the lower series of the Triassic and the Salt Range sequence of zones presented as the type section. Later, Noetling (1901) reaffirmed the pre-eminent importance of the Salt Range sequence in Scythian chronology, at the same time modifying somewhat the scheme of zones proposed by Waagen. It was not until 30 years later that it was generally recognized that the Triassic fossil-bearing formations in the Salt Range studied by Wynne (1878), Waagen (1895), and Noetling (1901, 1905) encompassed only the lower half or so of the Scythian. Waagen's Salt Range ammonites, however, have continued to play a dominant role in our interpretation of the evolution and systematics of Scythian ammonoids.

Five months of the winter of 1961–1962 were spent in the Salt Range, studying the Triassic formations throughout the Salt Range and in the Trans-Indus ranges (Figs. 1, 2). During much of this period and on occasional short subsequent visits, Dr. Curt Teichert was occupied with a study of the Permian formations. A study of the Permo-Triassic boundary beds was undertaken as a joint project between Teichert and myself.

Teichert (1966) has presented the results of his study of the Permian "Productus limestone" of the Salt Range. The present report deals with the Triassic formations of the Salt Range and Surghar Range. The paleontological portion of this paper is restricted to new faunas from the upper part of the marine portion of the Triassic formations. Complete restudy of the faunas first described by Waagen (1895) is in progress; however, the numbers of species and specimens are very large, and further time is needed to complete this portion of the study. The fauna described here establishes a late Scythian age for the upper part of the "Ceratite Formation" of Waagen.

ACKNOWLEDGMENTS

HISTORY OF RESEARCH

The first serious study of the succession of strata in the Salt Range of West Pakistan was carried out by Andrew Fleming in the middle of the 19th century. One of the more important aspects of Fleming's work in the Salt Range was the collection of a suite of fossils. These were sent to England and were studied and described by such contemporary celebrities as Sir Roderick Murchison and Thomas Davidson in England, E. de Verneuil in France, and L. de Koninck in Belgium. It was the suite of fossils studied by de Koninck (1863) that provided the first indication of the "Secondary formations" in the Salt Range. The circumstances can best be related in de Koninck's (1863, p. 1) own words:

> "Among these fossils, certain species belong to genera that have hitherto only been found in the Secondary formations, and occur principally in the lower groups of that great geological period. Such, above all, are the *Ceratites*, which appear to be tolerably abundant in a rock of the Punjaub Salt-range, and are remarkable from the fact that they are all new to science. But for this last circumstance, one might have entertained serious doubts relative to their geological position, although Dr. Fleming had ascertained by personal examination that they occurred in the same beds as those which contained the Carboniferous *Producti* and *Spirifirae*. At all events there is still this

Figure 1. Map of West Pakistan showing location of area studied for this report.

> remark to make, that the rock which contains the *Ceratites* has not shown me (at least in relation to the specimens confided to my examination) any traces of those other Palaeozoic genera. It is therefore to be desired that new observations should be brought to confirm those already made by the learned Edinburgh Doctor, who was the first to throw some light on the geological constitution of the ancient kingdom of Runjeet Sing."

The first comprehensive report on the geology of the Salt Range was by A. B. Wynne (1878) of the Geological Survey of India. Wynne carried out his field studies of the Salt Range and Surghar Range between 1869–1872. During the later stages of his study, after he had completed his mapping, he was joined by W. Waagen, who, with Wynne, made further stratigraphic observations and collected additional faunas. Wynne's (1878) report contains the only detailed account of their stratigraphic observations. It has been extremely difficult for later Triassic students to interpret Wynne and Waagen's stratigraphy and to understand the spatial distribution of Waagen's ammonites. Because these strata and their faunas have such an important bearing on our understanding of this part of the Trias-
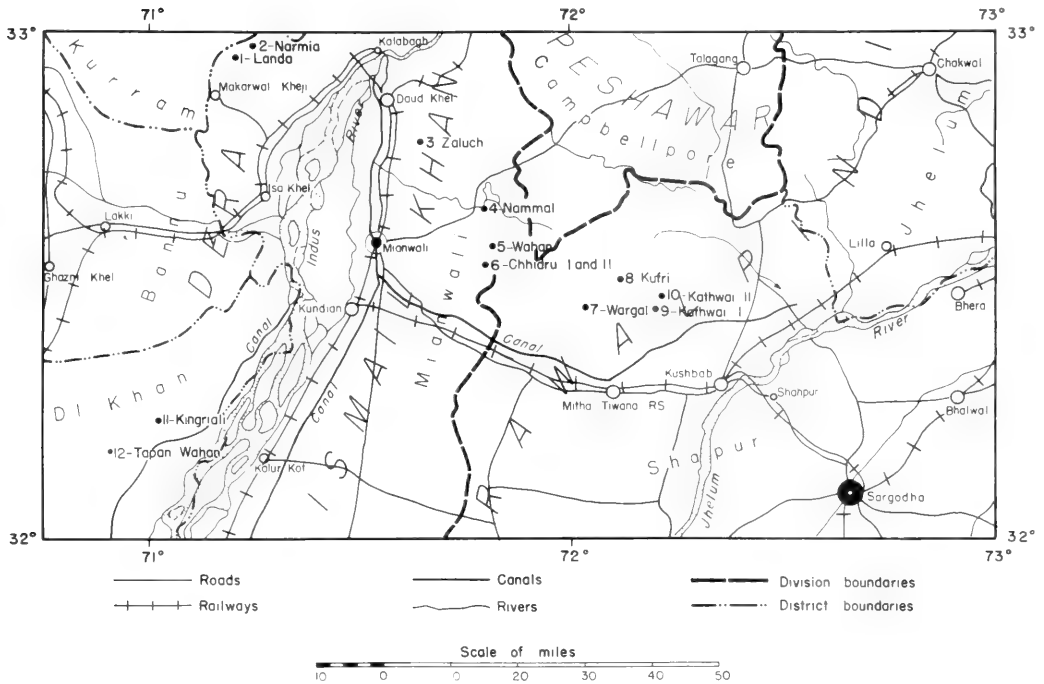
Figure 2.   Map of part of the Salt Range and Trans-Indus Ranges of West Pakistan showing localities of the stratigraphic sections.

sic column, it is necessary to review in detail the Wynne-Waagen data so that the stratigraphic and paleontological data published to date can finally be clearly understood (Fig. 3).

These authors observed that the Triassic strata make their appearance around Kathwai in the central Salt Range, and from there westward to the Trans-Indus ranges these strata are amply developed and thickened. In the region of Kathwai, Wynne and Waagen measured the following section (Wynne, 1878, p. 218):

		Feet
	Greenish and gray shales, variegated, red, yellow and blue at top; *Ceratites*	20–30
Trias	*Ceratite* limestone	3–4
	Yellow, sandy calcareous beds with *Rhynchonellae*	5

Brown dolomite, like that at Pail   3
Gray and greenish calcareous

Carbon-iferous	and micaceous sandstone, with limestone bands, weathering red in parts and containing *Bellerophon, Productus*, etc.	90–100

Approximately six miles west of Kathwai in the vicinity of Jalar (Jalhar) Waagen measured the following section (Wynne, 1878, p. 224):

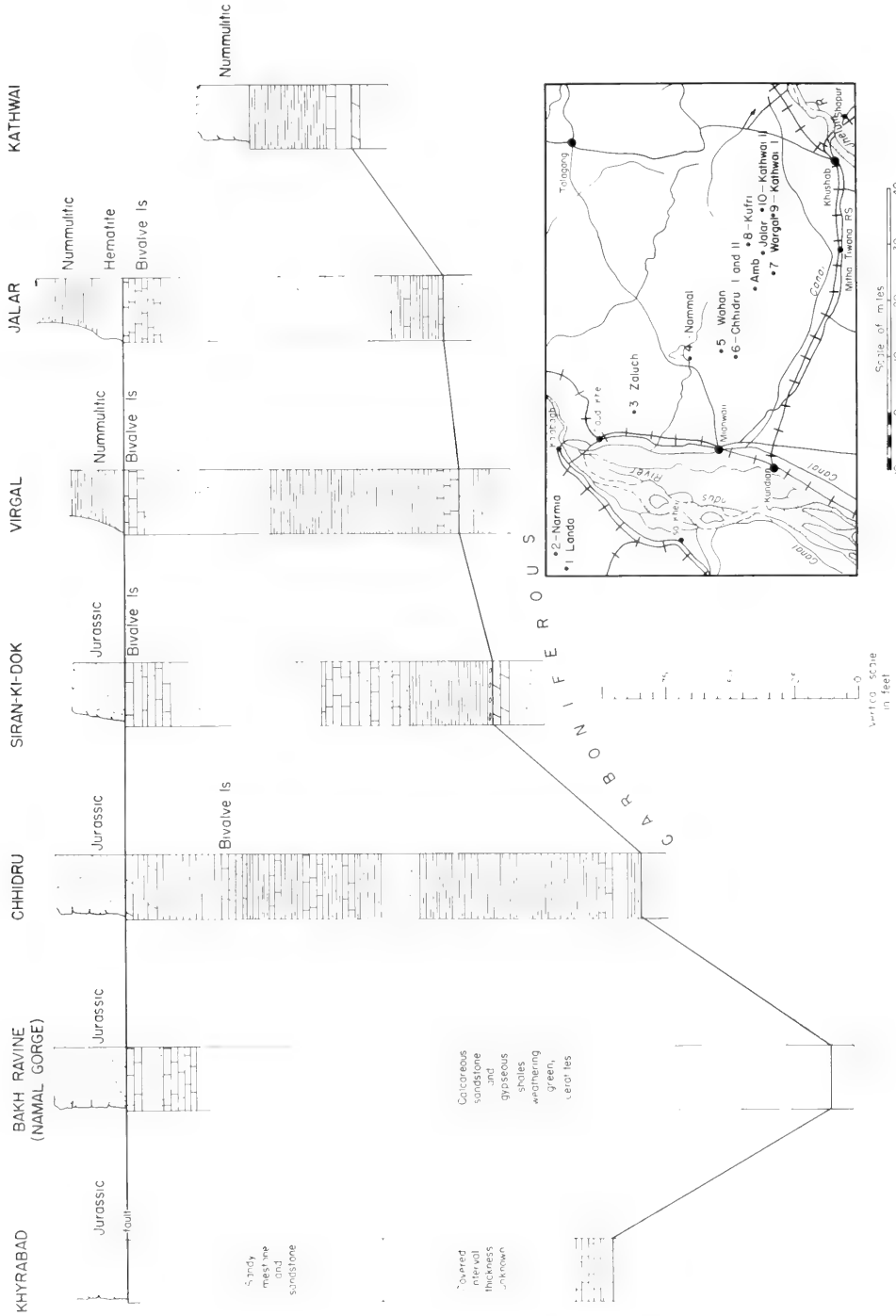|		Feet
	Hard limestones with Bivalves (overlain by "Hematite," marls and limestone beds Waagen assigned to the Nummulitic).	4–5
	Thin-bedded hard limestone with different species of *Ceratites*	10
Trias	Brown sandstone with *Ceratites Flemingi*	10
	Brownish and light yellow sandstone with few *Ceratites*. In the upper part of these sandstones is the *Bel-*	

Figure 3. Diagrammatic representation of the sections of Triassic strata measured by Wynne (1878) and Waagen in the Salt Range of West Pakistan.

lerophon bed of this *Ceratite*
group.   80
Ceratite marl and hard thin
Ceratite limestones   20

| Carbon-iferous | Brown sandstones and sandy limestones of the *Bellerophon* group, very thick | 100–150 |

Approximately four miles to the south and slightly west of Jalar, Waagen (*in* Wynne, 1878, p. 225) recorded the following sequence assigned to the Trias exposed near the village of Virgal (Wargal):

		Feet
Trias	Grey limestone with numerous Bivalves (overlain by sandstone beds assigned by Waagen to the Jurassic).	2
	Thin-bedded hard sandy limestone, no fossils	6
	Ceratite sandstone, thin-bedded, soft yellow sandstone with gypsum; a *Bellerophon* bed in the upper region.	50
	Green *Ceratite* marls	60–70
	Thin-bedded limestone with *Ceratites*	8

Carbon-iferous	Grey sandstone layers	6
	Black coaly, shaly beds, micaceous	3–6
	Thick light grey concretionary sandstone with nests of fossils, small *Producti*, *Bellerophon*, and *Gastropoda*	6

Near the village of Amb, Wynne and Waagen measured a thick stratigraphic sequence from the Speckled sandstone through the Nummulitic formations. They assigned 160 feet of this sequence to the Triassic recognizing a Lower Ceratite limestone and a Ceratite marls unit, combined the upper part into a limestone and sandstone unit but gave no details as to the relative thickness of their divisions (Wynne, 1878, p. 238).

High up in the Amb valley near a village of Seran-ki-dok (a locality not located by the writer nor known to the natives at the present time), Wynne and Waagen measured the following fairly detailed sequence of the Triassic (Wynne, 1878, p. 243):

		Feet	Inches
Trias	Very hard rusty limestone with numerous sections of *Ceratites* or *Ammonites*, gastropods and bivalves (overlain by sandstone beds assigned by Wynne and Waagen to the Jurassic).	3	0
	Soft yellow sandy beds	3	0
	Hard rusty-colored layer	1	6
	Grey cavernous sandstone	3	0
	Very hard grey limestone, glauconite, and bivalves	6	0
	Soft yellow sandstone	60	0
	Thin bed of sandstone with many indistinct bivalves	0	3
	Hard brown bed with numerous pebbles of limestone	1	6
	Grey limestone with numerous bivalves	3	0
	Thin-bedded limestone with *Ceratites*	10	0
	Sandstone and limestone with *Ceratites*	20	0
	Ceratite marl, badly seen	30	0
	Brown conglomerate bed	1	6
	Total	142	9

| Carbon-iferous | Rusty dolomite | 6 | 0 |
| | Light colored sandstones, *Bellerophon*, *Athyris subtilita*, *Dentalium*, etc. | | |

Another fairly detailed section measured at a locality stated to be "east-by-north of Chideru," which I interpret to be Chhidru Nala, was measured by Waagen (Wynne, 1878, p. 248, 249):

		Feet
Trias	Hard rusty dolomite with a *Cardinia* and *Anoplophora* (overlain by sandstone beds Waagen considered as perhaps the base of the Jurassic)	3
	Green marls	6
	Rusty dolomite	3
	Green sandy marls, with sandy layers and gypsum	20–30
	Hard limestone with many bivalves	3
	Rusty sandstone, fucoids	3
	Grey sandstone with *Ceratites*, *Gervillia*, *Orthoceras*	3
	Rusty sandstone, with fucoids	2
	Grey marls with flaggy limestone	2
	Grey marls, nodular marls, and	

		Feet
	hard limestones, with spinose *Ceratites*	50
	Ceratite sandstone, not clearly seen, with extremely large species of *C. Flemingii*	10–20
	Green Ceratite marls	60–80
	Flaggy lower Ceratite limestone	3–5
	Grey sandstone	6
	Green marls	4–5

Carbon-iferous	Yellow soft sandstones with concretions; filled with fossils, *Bellerophon*, *Athyris*, *Dentalium*, *Herculaneum*, etc.	

Between the latitude of Chhidru and Nammal Gorge, Wynne (1878, p. 251) recorded 300 to 350 feet of "Green shaly and flaggy limestone and sandstone beds" of Trias age. This locality Wynne states as the Bazar River valley which is the upper part of the Khaji Wahan Nala.

In and along Nammal Gorge (called Bakh Ravine by Wynne), these authors record the following sections (Wynne, 1878, p. 254, 255):

		Feet
	Thin grey limestones	6
	Sandstones	8
Trias	Thin grey limestones with *Ceratites*	13
	Calcareous sandstones and gypseous shales, weathering green, *Ceratites*	250
	Total	277

Carbon-iferous	Thin-bedded limestones and shales, sandy limestones, thick-bedded black and dark-colored limestones with a few shales, *Goniatites*, *Orthoceras*, *Spirifer*, *Productus*, *Fenestella*, *Terebratula*, Crinoids, etc.	250–300

Between Nammal Gorge and the Indus River, Wynne (1878) noted a number of Trias exposures but described them only in terms of the vaguest generalities. At Khyrabad, just east of the Indus River, Waagen measured the following sequence of Trias strata (Wynne, 1878, p. 263):

		Feet
	Very hard, brown sandy limestone and sandstone (overlain by sandstone of possible Jurassic age in fault contact, according to Waagen)	100
Trias	Space covered by debris	
	Glauconitic limestone with *Ceratites*	6–10
	Sandy marly bed	1
	Thin-bedded brown limestone, with *Rhynchonellae* and *Ceratites*	3

Carbon-iferous	Grey sandstone, with *Bellerophon* and *Dentalium*, badly seen.	

Wynne's report on the ranges to the west of the Indus River, including among others the Surghar and Khisor ranges, was not published until 1880. This report contains little detailed stratigraphic data regarding the Triassic formations. Wynne's general conclusions on these strata can be best summarized in his own words:

> "*The triassic Ceratite group*—Is as usual to the east stratigraphically simply a superior part of the carboniferous formation. It always accompanies the latter here, and it shows the same characteristic thin-bedded gray limestone and greenish gray shales or clays by means of which it was first distinguished in the west Salt Range sections. Its *Ceratites* are in some places numerous, in others large, and its whole aspect is that which it presents on the other side of the Indus, without any strongly marked line of stratigraphic demarkation separating it from the paleozoic beds" (Wynne, 1880, p. 240–241).

The data from the Trans-Indus ranges in Wynne's report are too incomplete to incorporate on a stratigraphic profile; however, the data for the Salt Range are diagrammed on Figure 3. In view of Waagen's subsequent writings on these Triassic strata it is of interest to note the vagueness of the lithofacies units he later recognized and the absence of reference to the Triassic strata above the Bivalve limestone to which he later referred.

Waagen's own descriptions of the rock formations exposed in the Salt Range did

not appear until 1889, when he published the geological results to his monograph on Salt Range fossils. For the Triassic formations he introduced a three part division. His descriptions and comments of these units can now be understood and are quoted here (Waagen, 1889, p. 49, 50):

"Ceratite Beds

"It is somewhat doubtful whether these beds can rightly be considered as a single group, as petrographically they are always composed of three different divisions. At the base there are thin-bedded hard light-grey limestones, then follow greyish-green thick marls with some limestone beds full of fossils, and at last there comes a thick yellow sandstone with large ceratites. The distribution of these three divisions is not absolutely identical; the hard lower limestones make their first appearance in the country east of Khoora, the marls near Katruhee, and the sandstones near Jalar. On the whole, however, these beds are so intimately connected that it will be best to treat them as a whole under a common name.

"After they have made their appearance, the development of these ceratite beds is very uniform all over the Salt-range, and somewhat different sections are only to be met with in the north, in the Tredian hills. The dislocations in this country are, however, so enormous that it remains doubtful whether the differences there are not solely caused by parts of the sections being concealed by faults.

"The ceratite beds are always in perfect concordance with the underlying strata, so that, according to Mr. Wynne, they form stratigraphically a group perfectly inseparable from the Upper Productus limestone, and exhibiting a marked difference from the latter solely by their fossil contents. I perfectly concur in this respect with Mr. Wynne.

"Grey Bivalve Limestone

"The thickness of this group is nearly always very insignificant, but as it contains an apparently rather singular fauna, it seemed to me practicable to distinguish it on palaeontological grounds. It is generally composed of hard grey limestones, with countless remains of bivalve shells, which can, however, only at a few places be removed from the rock. The first place where this group has been observed by me was near Jalar. From this place towards the west the group is everywhere present, though not conspicuous. It rests everywhere conformably upon the ceratite sandstones of the preceding group, and can most easily be distinguished. Trans-Indus, its existence has not yet been proved, but it is probable that it will be also here represented.

"Grey and Yellow Dolomites

"It is only quite in the western districts that this group has been observed. The first traces of it have been found by me in the country around Chidroo, where, however, its thickness is as yet not more than 20 to 30 feet. In the Tredian hills its thickness is somewhat more considerable. It is chiefly composed of grey or rusty or yellow dolomites, with some green sandy marls. To these are added some variegated sandstones in the Trans-Indus extension of the Salt-range, where the group attains its greatest development up to a thickness of 250 feet and more.

"Everywhere I have observed the group, it rests conformably on the Bivalve limestones. Fossils are always scarce, and only some bivalves, gasteropods and a single ceratite have been found up to the present."

Waagen offered no discussions on the age of his units, but on a table (Waagen, 1889, p. 57) he placed the Ceratite beds in the Lower Triassic with question, the grey bivalve limestone in the Middle Triassic with question, and the grey and yellow dolomites in the Upper Triassic with question.

Waagen's next contribution on the Salt Range Triassic formations appeared in 1892, one version published in Vienna in German, and a modified translation in English by the Geological Survey of India. In these papers Waagen first divided the Ceratite Formation, into Lower Ceratite limestone, Ceratite marls, Ceratite sandstone, and Upper Ceratite limestone. For the uppermost unit, which he previously called the grey and yellow dolomites, he introduced the name Dolomite group, designating the upper part of this unit as the "Topmost limestone." Likewise in these publications Waagen offered more data on age assignments of these beds. He (1892b) recognized five faunal units in the interval from the Lower Ceratite limestone through the Ceratite sandstone. He felt that the difference in faunas between the Ceratite sandstone and the Upper Ceratite limestone reflected

a significant stratigraphic boundary. All the units below this boundary were thus considered as equivalent to the Bunter sandstone of Europe. Waagen was not explicit as to why he came to this conclusion. It would appear that this age determination was derived from his conclusion that the Upper Ceratite limestone, and the Bivalve limestone were equivalent to the Muschelkalk of Europe. Again it is not at all apparent on what basis Waagen arrived at that conclusion. The age of the Dolomite group was decided on the basis of a single ammonite specimen which Waagen considered as "so nearly related to the genus *Tropites*" and gave the name *Pseudharpoceras*. The recognition of this specimen as a tropitid led Waagen to conclude that the Dolomite group was of Keuper age. He specifically excludes a Rhaetic age for any part of this unit, believing this to be represented within the overlying Variegated Series. This particular specimen will be discussed in detail later in this paper, but it should be pointed out that it was collected by Dr. Verchere from a yellow limestone "placed at the base of the Variegated (Jura-Rhaetic) Series at the limit of the Ceratite Formation" in the Sheik-Budin Hills of the Trans-Indus region. It is the only ammonite described by Waagen from the Dolomite group. Considerable doubt has been expressed as to the horizon of this specimen.

In his monograph on the "Fossils of the Ceratite Formation," Waagen (1895) again described the stratigraphic units of the Triassic formations and used the following nomenclature:

In this treatment of the Triassic formations Waagen used specific names for the three lithofacies units of the Ceratite beds, separated out the Upper Ceratite limestone and recognized two vague divisions in his upper dolomite unit. A very strange aspect of the 1895 monograph by Waagen is an absence of any discussion of the age and correlation of the Salt Range fauna from the Ceratite Formation. In the introductory pages of this monograph Waagen is evasive on the matter of age and correlation but does imply that these questions were to be discussed in a chapter on "geological results," a chapter which has never been published. A discussion of the zonal divisions and correlations of the Salt Range Ceratite Formation appeared in the same year in the classic paper by Mojsisovics, Waagen, and Diener (1895); this contained their proposal for a stratigraphic classification of the Triassic. Waagen and Diener prepared the section on the lower half of the Triassic and their scheme of classification is given in Table 1.

Waagen and Diener introduced the name Scythian in this paper. They recognized seven zones within the Scythian and used the Salt Range sequence of the Ceratite beds as the type section because it included six of the seven zones. The only zone absent in the Salt Range, that of *Otoceras woodwardi*, was known to them from the Himalayas. Under this scheme of classification one zone was recognized as encompassing the Lower Ceratite limestone, two the Ceratite marls, and three the Ceratite sandstone.

The Upper Ceratite limestone was assigned a zone unto itself, that of *Stephanites superbus*. Waagen was greatly impressed

Dolomite Group	{ Topmost limestone { Dolomite beds	
Bivalve Limestones	{ Bivalve beds { Upper Ceratite limestone	
Ceratite Beds	⎰ Ceratite sandstone	{ *Flemingites flemingi* beds { *Stachella* (*Bellerophon*) beds { Lower sandstone beds
	⎱ Ceratite marls Lower Ceratite limestone	

Table 1. Zonal scheme for the lower half of the Triassic system for the Tethyan realm suggested by Mojsisovics, Waagen, and Diener (1895)

Series	Stage	Substage	Mediterranean Trias Province — Zone Tethyan facies	Mediterranean Trias Province — Formations	Indian Trias Province — Zone Tethyan facies	Indian Trias Province — Formations
Dinarian	Anisian	Bosnian	Zone of Ceratites trinodosus	U. Muschelkalk	Zone of Ptychites rugifer	Muschelkalk of the Himalayas
		Balatonian	Zone of Ceratites binodosus	L. Muschelkalk	Zone of Sibirites prahlada	Beds with Rhynchonella griesbachi in the Himalayas
Scythian	Hydaspian		Zone of Tirolites cassianus	Werfen Beds	8. Zone of Stephanites superbus	Upper Ceratite limestone, Salt Range
	Jakutian				7. Zone of Flemingites flemingianus	Ceratite sandstone, Salt Range / Subrobustus beds, Himalayas
					6. Zone of Flemingites radiatus	
				Eastern Alps	5. Zone of Ceratites normalis	
		Gandarian			4. Zone of Proptychites trilobatus	Ceratite marls, Salt Range
					3. Zone of Proptychites lawrencianus	
	Brahmanian				2. Zone of Gyronites frequens	Lower Ceratite limestone, Salt Range
		Gangetian			1. Zone of Otoceras woodwardi	Otoceras beds, Himalayas

by the dominance of trachyostracan ammonites in the Upper Ceratite limestone and reiterated the thought that the first significant break in the sequence of the Ceratite Formation came between that unit and the underlying Ceratite sandstone. No mention was made in this report of the age of the Dolomite Group.

Waagen's work on the stratigraphy and paleontology of the Ceratite beds was subjected to a series of highly critical attacks by Fritz Noetling. This author states (Noetling, 1901, p. 370) that he spent the winter of 1893–94, November, 1898, and finally the winter of 1899–1900 in the Salt Range. At first, Noetling (1900a) maintained that the Ceratite Formation must be included in the Permian System because the gradual passage from the Productus limestone to the Ceratite beds made assignment of these units to two different eras impossible. In addition, he reported the presence of *Otoceras* from the Ceratite marls, which he then correlated with the Himalayan *Otoceras* beds, and assigned a Permian age to all these beds (Noetling, 1900b).

The identification of *Otoceras* in the Salt Range was soon retracted. Griesbach, the discoverer of the *Otoceras* fauna in the Himalayas, assigned the fauna to the Lower Triassic (Griesbach, 1880). Also, Mojsisovics (1892 a, b) came to the conclusion that it is "most probable" that the *Otoceras* beds formed the base of the "Bundsandstein" and are closest to the boundary of the Permian.

Noetling received support in his views on the stratigraphic position of *Otoceras* from A. v. Krafft (1900, p. 203), who, in a preliminary report on the stratigraphy of the Spiti region, correlated the *Otoceras* beds there with the Ceratite marls and the Lower Ceratite limestone of the Salt Range. In the following year, Krafft (1901) changed his interpretation considerably. He divided the strata exposed between the Kuling shale and the *Hedenstroemia* beds in the Spiti region into three zones: the *Otoceras* bed, the *Ophiceras* bed, and the *Meekoceras* bed.

The *Meekoceras* bed he referred to the Triassic, the age of the *Ophiceras* bed was left in doubt, and the *Otoceras* bed was correlated with the Upper Productus limestone on the strength of the identification of *Medlicottia* (*Episageceras*) *dalailamae* Diener with *Medlicottia wynnei* Waagen from the zone of *Euphemus indicus* in the Salt Range. Diener (1901b) refuted this argument, rejecting the identity of these two species of *Medlicottia* (*Episageceras*).

In 1901, Noetling published a long paper on the Permian and Triassic formations of the Salt Range, in which he presented stratigraphic data on the section at Chhidru and Virgal (Wargal) and introduced a zonal scheme. Noetling's Chhidru section is along the east side of the nala at a site called Mittiwali (Noetling called it Mittiali), a section also studied by the author; Noetling's description of this section is as follows (the numbers are in Noetling's original section and only part of the Upper Permian strata are included):

		Thickness	
		Feet	Inches
26.	Sandstone, white, sandy	26	0
25.	Sandstone with *Stachella*	5	0
24.	Limestone, olive, thin-bedded, platty, hard, with thin shale interbeds. Contains numerous examples of *Stephanites superbus* Waagen, *Prionites tuberculatus* Waagen, *Acrochordiceras distractus* Waagen	50	0
23.	Sandstone, olive, brownish, hard, containing numerous specimens of *Flemingites flemingianus* Waagen, *Hedenstroemia* spec. (new), *Aspidites superbus* Waagen	10	0
22.	Marl, dark green, thin-bedded, thin beds of limestone, fossiliferous, containing *Koninckites volutus* Waagen, *Prionolobus rotundatus* Waagen, *Celtites* spec. and many other species	100	0
21.	Limestone, dark brown, hard, flaggy, with numerous poorly preserved fragments of ceratitic ammonites	3	0
20.	Marl, green, unfossiliferous	2	0
19.	Limestone, dark brown, hard, flaggy, with numerous poorly preserved ceratitic ammonites	5	0

18. Sandstone, light brown, calcareous, thin-bedded, with argillaceous layers _____ 2   6
17. Limestone, rusty brown, hard, ringing under hammer, with indistinct traces of ammonites _____ 0   4
16. Sandstone, light brown, with argillaceous interbeds _____ 3   0
15. Sandstone, dark, hard, full of fossil fragments, probably *Bellerophon* or *Stachella* _____ 0   6

Noetling (1901, p. 453) stressed the conformity of these strata and concluded, after an extensive discussion, that the Permian-Triassic boundary lay between beds 16 and 17.

Noetling's (1901, p. 454) Virgal (now Wargal) section is really too generalized to be of much help. He records 18 feet of Lower Ceratite limestone overlain by 120 feet of marls which are presumably part of the Ceratite marls.

It appears that Noetling's views on the Triassic formations of the Salt Range were formulated mainly from his studies at Chhidru and Virgal (Wargal). In terms of the stratigraphic divisions recognized by Waagen (1895), Noetling concluded that the Dolomite Group was not Scythian in age (a view never held by Waagen); that the Ceratite sandstone of Waagen was merely a sandy facies of the Upper Ceratite limestone; that the Bivalve beds of Waagen in general did not exist. He (Noetling, 1901) then introduced the following zonal scheme (Table 2). (His zones for the Upper Permian Chhidru Group are included, as they have bearing on correlation problems of these strata.)

This scheme represented a considerable revision of Noetling's previous views, a fact commented upon by Diener (1901a). Noetling considered this zonal scheme to represent "die Gliederung der Skythischen Stufe von oben nach unten." In the single zone for the Upper Ceratite limestone he was in agreement with Waagen, but for the Ceratite sandstone he considered one zone as representative rather than the three recognized by Waagen. He was influenced

in this conclusion by the following observations: (1) *Stachella* was not confined to the mid part of the Ceratite sandstone but was also present in the Ceratite marls and the Upper Ceratite limestone; (2) *Ceratites normalis* (the zonal index for the lower part of the Ceratite sandstone according to Waagen) was established for a poorly preserved fragmentary specimen that could not be identified; and (3) *Flemingites radiatus* (the zonal index for the middle part of the Ceratite sandstone, the horizon of *Stachella* according to Waagen) was nothing more than the inner whorls of *Flemingites flemingianus*. The substitution of two different zonal index species for the Ceratite marls was based on his objection to the poor state of preservation of Waagen's species. According to Noetling, the zone of *Koninckites volutus* encompassed the greater part of the Ceratite marls, and the zone of *Prionolobus rotundatus* was confined to the basal beds of the unit. For the Lower Ceratite limestone, Noetling objected to Waagen's narrow conception of the genus *Gyronites* and its separation from *Xenodiscus*.

In this same 1901 paper, Noetling correlated his zone of *Flemingites flemingianus* and the zone of *Koninckites volutus* with the *Hedenstroemia* beds of the Himalayas, and the zone of *Prionolobus rotundatus* and the zone of *Celtites* sp. with the zone of *Meekoceras lilangense* of the Himalayas. He then considered the two uppermost zones of his Chideru (Chhidru) Group (that of *Euphemus indicus* and *Medlicottia wynnei*) as correlative with the *Ophiceras tibeticum* Zone of the Himalayas, and the zone of *Bellerophon impressus* as equivalent to the *Otoceras woodwardi* Zone of the Himalayas. It is of interest to note that in this same paper Noetling (1901) offered as an explanation for the extinction of the Permian brachiopod fauna the change from deeper water conditions in the Permian to shallower water in the Triassic; the deep water brachiopods died out and were re-

TABLE 2.   ZONAL SCHEME FOR UPPER PERMIAN AND LOWER TRIASSIC FORMATIONS OF THE SALT RANGE, WEST PAKISTAN, AFTER NOETLING (1901)

Scythian	Upper Ceratite limestone	Zone of *Stephanites superbus*
	Ceratite sandstone	Zone of *Flemingites flemingianus*
	Ceratite marls	Zone of *Koninckites volutus* Zone of *Prionolobus rotundus*
	Lower Ceratite limestone	Zone of *Celtites* (?) sp.
Thuringian Stage	Chideru Groups (now Chhidru)	Zone of *Euphemus indicus* Zone of *Medlicottia wynnei* Zone of *Bellerophon impressus* Zone of *Cyclolobus oldhami* Zone of *Derbyia himisphaerica* Zone of *Productus lineatus*

placed by ammonites, which preferred near-shore water conditions.

Noetling's last contribution on the Salt Range, which appeared in the Lethaea Geognostica (1905), repeated the stratigraphic data given in 1901, but he made some additions to his previous interpretations. First, he accepted the Ceratite sandstone as a lithostratigraphic unit of independent status. For the zone of the Lower Ceratite limestone, he introduced the name of *Celtites radiosus* (Koken manuscript) Frech, and he introduced a new zone, that of *Celtites fallax* (Koken manuscript) Frech, encompassing the middle part of the Ceratite marls. Noetling likewise maintained that the sequence of Permian and Triassic strata in the Salt Range represented continuous deposition. At this time he suggested that an increase in the temperature of the sea was responsible for the extinction of the brachiopods. In fact, to explain the absence of brachiopods in the *Otoceras* beds of the Himalayas (which he considered Permian in age), Noetling suggested that the change in temperature progressed from the north to the south, thus affecting first the Himalayan region, while the brachiopods persisted in the Salt Range.

In the early 1930's E. R. Gee mapped the entire Salt Range on the scale of 2 miles to 1 inch. His maps have not yet been published, but are available for study and in-

spection in the archives of the Geological Survey of Pakistan in Quetta. In the intervening period, between the time of Noetling's publications and Gee's mapping, the only significant writing on the Triassic Formation of the Salt Range was offered by Diener (1912), who gave a splendid review of the boundary problem and the age of *Otoceras*.

Although Gee's maps of the Salt Range remain, as yet, unpublished, he did publish occasional observations. In one of these, Gee (1947, pp. 143–147) presented a detailed description of the stratigraphic section in Nammal Gorge (Bakh ravine of Wynne's report); the Triassic formations there are described as follows:

```
                                          Feet
Trias (?)  361–366 feet
  Kingriali Dolomites  (186–188 feet)
    (e)  Hard, dark grey, splintery lime-
         stone ...................................    14
    (d)  Light grey and yellowish, mas-
         sive, fine-textured, hard splintery
         limestones,  and  dolomitic  lime-
         stone  weathering  vesicular  near
         the base.  Some fossils visible but
         difficult to extract ...................   147
    (c)  Sandy, red, ferruginous band ....     1
    (b)  Yellow-grey,    falsebedded,   cal-
         careous sandstone .....................    14
    (a)  Yellow brown, hard, bedded lime-
         stone ...................................  11–12
  Kingriali Sandstones  (238–242 feet)
    (f)   Grey and greenish sandy shales ..    4–5
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(e)   Hard, dark-brown, calcareous
     sandstone and impure limestones   1–3
(d)   Massive grey and yellowish me-
     dium-textured sandstone with 3
     to 4 feet carbonaceous shale
     band in the middle _____   115
(c)   Grey and ferruginous, purplish-
     brown, ripple-marked sandstones
     alternating with purplish-brown
     shales and micaceous flags with
     plant fragments, the shales pre-
     dominate in the lower part _____   55
(b)   Hard, fine-textured, greenish-grey
     weathering russet-brown lime-
     stone __ _____ ____ _____ _____   3–4
(a)   Grey and greenish-grey shales al-
     ternating with brownish-weather-
     ing limestones and sandstones ____   50
     Hard grey and brownish lime-
     stone _____ _____ _____ _____   10
     (comformable transitional junc-
     tion) __ _____ __ _____ ___ ___

Trias (343–345 feet)
   Ceratite Beds
(f)   Grey and purplish, calcareous
     sandstones, flags and shales alter-
     nating, about one half is shale ____   64
(e)   Grey and greenish grey shales
     with flaggy grey-green sandstone
     bands _____   42
(d)   Grey and brownish-grey bedded
     limestone with shale bands, and
     including numerous badly pre-
     served fossils _____   5
(c)   Grey-green shales with flaggy,
     grey, *Ceratite*-bearing limestones
     alternating; limestones prominent
     in lower half _____   51
(b)   Dull green and flaggy sandstone
     shales with a few limestone bands,
     shales predominate _____   117
(a)   Flaggy, grey, *Ceratite* limestone   4–6
     (Base of Trias apparently conformable
     to Upper Productus beds, top of the
     latter is weathered russet-brown)

Permian
   Productus Limestones (703–723 feet)
   Upper Productus beds (226 feet)
(c)   Brownish-grey, weathering russet-
     colored, hard arenaceous lime-
     stone   ____ _____ ___ _____ _____   6
(b)   Soft grey sandy shale _____   2.5–3

Additional observations by Gee on the
Triassic formations of the Salt Range were
published by Pascoe (1959). In this report
the name Mianwali series was introduced
to include the three units recognized by
Gee in 1947, namely the Ceratite beds,

Kingriali Sandstones, and the Kingriali Dolo-
mites.

Schindewolf (1954) studied the Permian-
Triassic contact beds on the west side of
Chhidru Nala and presented a measured
section of the boundary strata essentially
the same as that by Kummel and Teichert.
Schindewolf's most important contribution
to knowledge of the Triassic System was
the discovery of *Ophiceras connectens* in
beds below the Lower Ceratite limestone.

PRESENT INVESTIGATION

The adoption of a modern stratigraphic
code by the Geological Survey of Pakistan
as a guide for future geologic studies in
Pakistan has required the introduction of a
modern nomenclature for the Triassic for-
mations of the Salt Range and Trans-Indus
ranges. A modern nomenclature for some
of the Permian and Triassic formations of
the Salt Range has been introduced by
Kummel and Teichert (1966 a, b) and is
shown here on Table 3.

In the course of my own studies, seven
sections of Triassic rocks were studied in
detail (Fig. 4). These range from one at
Kathwai in the most eastern outcrop area
of the Triassic formations in the Salt Range
to Landa Nala and Narmia Nala in the
Surghar Range west of the Indus River.
Attention was focused mainly on the
Mianwali Formation which includes most
of the strata formerly referred to as the
Ceratite beds. Of the Tredian Formation
detailed study was made only of the Landa
Member. The Khatkiara Member has been
studied by Danilchik and Shah (in press)
and the Kingriali Dolomite by Gee (1947).

The detailed measured sections of the
Triassic formations for the seven localities
studied comprise Appendix I. A diagram-
matic representation of these sections is
shown on Figure 4 and a schematic facies
interpretation is shown on Figure 5.

MIANWALI FORMATION

The name Mianwali was first used by
Gee (*in* Pascoe, 1959, p. 852) in a time

TABLE 3. PERMIAN AND TRIASSIC FORMATIONS IN THE KHISOR RANGE, SURGHAR RANGE, AND SALT RANGE, WEST PAKISTAN

System	Series	Stage		Formation	Old Name
TRIASSIC	Upper?			Kingriali Dolomite (Gee, 1947)	Kingriali Dolomite (Gee, 1947)
	Middle?		Tredian Fm.[4]	Khatkiara Member[3]	Kingriali Sandstones (Gee, 1947)
				Landa Member[2]	
	Lower	Scythian	Mianwali Fm.[2]	Narmia Member[2]	Topmost ls. Dolomite beds (Waagen, 1895)
				Mittiwali Member[2]	Bivalve ls. (Waagen, 1895)
				Kathwai Member[2]	Ceratite beds (Waagen, 1895)
PERMIAN	Upper	Chhidruan		Chhidru Formation[1]	Upper Productus limestone (Waagen, 1879)
	Upper	Guadalupian		Wargal Limestone[1]	Middle Productus limestone (Waagen, 1879)
	Lower	Artinskian		Amb Formation[1]	Lower Productus limestone (Waagen, 1879)

[1] Waagen, 1891; emend. Noetling, 1901, and Teichert (in press).
[2] Kummel (in press).
[3] Danilchik and Shah (in press).
[4] Gee (in press).

stratigraphic sense for all rocks in the Salt Range believed to be of Triassic age. It is here proposed for a lithostratigraphic unit which is equivalent to the lower part of Gee's Mianwali series only.

The Mianwali Formation is the fossiliferous unit which has yielded all of the Triassic ammonites that have been described from the Salt Range. It comprises all the facies units (e.g. Lower Ceratite limestone through Topmost limestone) recognized by Waagen (1895). The formation represents a great wedge of varied facies, thickest in the west and thinning to the east. The thickest development of the formation studied is in Narmia Nala in the Surghar Range—635.5 feet (Fig. 4). In the easternmost areas of outcrop the formation is only 48.4 feet thick (at Kathwai), but here the section is truncated by erosion and overlain by the Dhak Pass Formation of Paleocene age. Complete development of the Mianwali

Formation is found in the Surghar Range and in the western part of the Salt Range at Zaluch and Nammal Gorge. In Chhidru Nala the upper part of the Narmia Member is truncated and overlain by the Murree Formation of Miocene age, but one mile further east the Mianwali Formation is complete, though its thickness is not known (Curt Teichert, written communication). At Kufri, the Kathwai Member and only 10 feet of the Narmia Member are preserved. From Nammal Gorge west to the Surghar Range, the Mianwali Formation is overlain conformably by the Landa Member of the Tredian Formation.

The contact of the Mianwali Formation with the underlying Chhidru Formation, of Upper Permian age, was a special project carried out in collaboration with Curt Teichert. Preliminary accounts of our studies of this extremely critical Permo-Triassic boundary have been prepared (Kummel and Teichert, in press), and no extended discussion will be given here. It is sufficient to state that we interpret the contact as a paraconformity but are not able to offer any concrete data as to the possible duration of the break in deposition in this area.

Kathwai Member

The lowest unit of the Mianwali Formation is a remarkably uniform dolomite and limestone bed present throughout the outcrop area of the Triassic formations in the Salt Range and in the Trans-Indus Ranges. Kummel and Teichert (in press) have recognized two units in the Kathwai Member, a lower dolomite unit and an upper limestone unit. The dolomite for the most part is finely crystalline with euhedral and anhedral grains. Some of the dolomite rhombs have been partly or entirely replaced by calcite. A large part of the rock unit consists of fossil fragments, mainly echinodermal, which are dolomitized, partially dolomitized or of recrystallized calcite. Fine-grained angular to subangular grains of quartz make up a small percentage of the rock, seldom as much as 10 per cent. The

individual bedded units of dolomite vary from massive to finely laminated; cross-bedding is not uncommon.

The upper unit of the Kathwai Member is a gray to brown, fine-grained limestone containing abundant shell fragments and echinoderm remains. The upper part of this unit is usually glauconitic and the lower part generally transitional with the underlying dolomite unit. This limestone unit is, like the dolomite unit, remarkably uniform throughout the area studied. Only at Chhidru and Munta Nala (Wargal) were some thin laminated sandstone beds present in the upper part of the unit.

The thickness of the Kathwai Member is also remarkably uniform. It is 7.5 feet thick at Narmia, 11.5 feet at Zaluch, 11 feet at Nammal Gorge, 16.8 feet at Chhidru, 15.5 feet at Kufri, and 12.5 feet at Kathwai.

Fossils are not uncommon in the Kathwai Member but at the same time are neither abundant nor well preserved. The most significant fossil is *Ophiceras connectens* Schindewolf which occurs throughout the member. In addition, a species of *Glyptophiceras* sp. indet. was found in the dolomite unit at Kathwai. These two species clearly indicate that the Kathwai Member is of lowest Scythian (*Ophiceras* zone) age. The remainder of the fauna of the Kathwai Member includes: lagenid-type Foraminifera; *Lingula* sp., rhynchonellids; pseudomotid, pectinid and other, indeterminate, pelecypods; crinoid and ophiuroid fragments, including one identified as *Ophioderma*? cf. *torrii* Desio by Hans Hess (written communication to Curt Teichert, 1964); *Miocidaris pakistanensis* Linck (most obviously and abundantly represented by spines); conodonts as reported by Huckriede (1958)[1]; fish teeth as reported by Waagen (1895). Bobb Schaeffer has examined samples from the dolomite unit exposed on the

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[1] W. C. Sweet is undertaking a monographic study of the conodonts from the Mianwali Formation; he reports (written communication) that conodonts are richly represented throughout the formation.
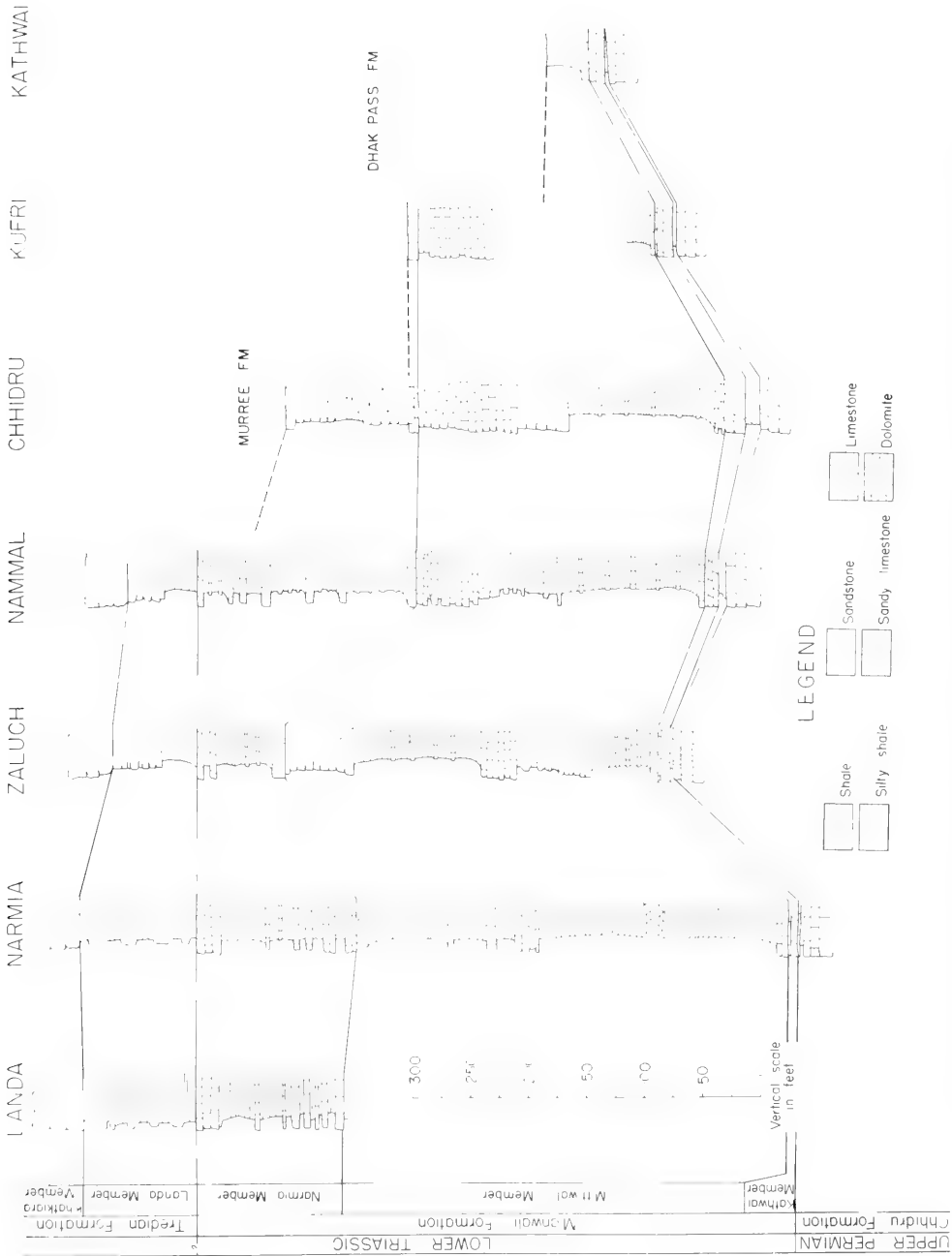
Figure 4. Stratigraphic sections of Lower and Middle? Triassic strata in the Salt Range and Surghar Range of West Pakistan.

east side of Chhidru Nala and was able to identify in these samples *Acrodus* sp., possibly one specimen of *Saurichthys* sp., but none of *Colobodus* nor *Gyrolepis* as recorded by Waagen.

The most surprising paleontological discovery from the Kathwai Member was the presence of brachiopods of genera otherwise known only from Permian rocks. In a preliminary paper (Kummel and Teichert, 1966b, in press), we have discussed these Permian brachiopods in detail. We were aided greatly in our studies by Dr. G. A. Cooper, who identified the brachiopods for us. For the present purpose I wish merely to give data on their occurrence and their interpretation. One specimen of a productid brachiopod was found on the east side of Chhidru Nala, six inches above the base of the Kathwai Member, in beds from which specimens of *Ophiceras connectens* had been found. Just west of Chhidru Nala, in Khan Zaman Nala, Teichert (personal communication) collected *Crurithyris* sp. (identified by G. A. Cooper) 5–6 feet above the base of the Kathwai Member. The largest number of these brachiopods was found in the lower 6–12 inches of the Kathwai Member in Narmia Nala. From collections made from this bed, G. A. Cooper has identified *Linoproductus* sp., *Spirigerella derbyi* Waagen, *Orthotetina* sp., *Enteletes* sp., *Martiniopsis?* sp., *Crurithyris* sp., *Lingula* sp., *Orthotichia* sp., and *Martinia* cf. *M. chideruensis* Waagen. As regards the age of these brachiopods, Cooper (written communication) writes as follows:

"Taking all of the information and putting it together I come to the same conclusion as previously. The presence of *Enteletes*, *Crurithyris* and *Orthotichia* suggests Lower or Middle Permian and the other named shells are inconclusive. Everything listed would be expected in earlier Permian than the Upper except the *Martinia* cf. *M. chideruensis*, the identification of which I am unsure. All of the assemblages are definitely Permian and I should say rather Middle Permian than Upper in aspect."

Cooper (personal communication) feels that all of the Permian brachiopods we sent him are the product of reworking. In this I am in full agreement. However, Teichert, only with the greatest reluctance, would accept the reworking hypothesis for the main brachiopod horizon at Narmia, but rejects this entirely for the Khan Zaman occurrence where *Crurithyris* was found 5–6 feet above the base of the Kathwai Member.

Mittiwali Member

The Mittiwali Member comprises the units Waagen (1895) designated as Lower Ceratite limestone, Ceratite marl, Ceratite sandstone and Upper Ceratite limestone. This member is 487.5 feet thick in Narmia Nala, 321.6 feet at Zaluch, 253 feet at Kufri, and only 40 feet at Kathwai in the eastern extremity of Triassic outcrops in the Salt Range. At the Kathwai locality the upper part of the Triassic sequence has been truncated by pre-Cenozoic erosion and the remnants existing are overlain by Paleocene limestone.

The lowest unit of the Mittiwali Member is a coquinoid limestone to which Waagen (1895) gave the name Lower Ceratite limestone. The unit is a gray, fine-grained limestone, with no glauconite, and containing a great abundance of ammonites, generally very poorly preserved. It is this unit which most previous authors, until Schindewolf (1954), placed at the base of the Salt Range Triassic sequence. Throughout the Salt Range this basal limestone unit is about five to six feet thick. In the Khisor Range, west of the Indus River, Teichert (personal communication) measured 25 feet for this unit. It is distinguished from the underlying limestone unit of the Kathwai Member by an absence of glauconite and a much greater abundance of fossils consisting almost entirely of ammonites, with occasionally a few pelecypods. The ammonites belong to the Gyronitan age of Spath (1934), the second zone in the sequence of Scythian
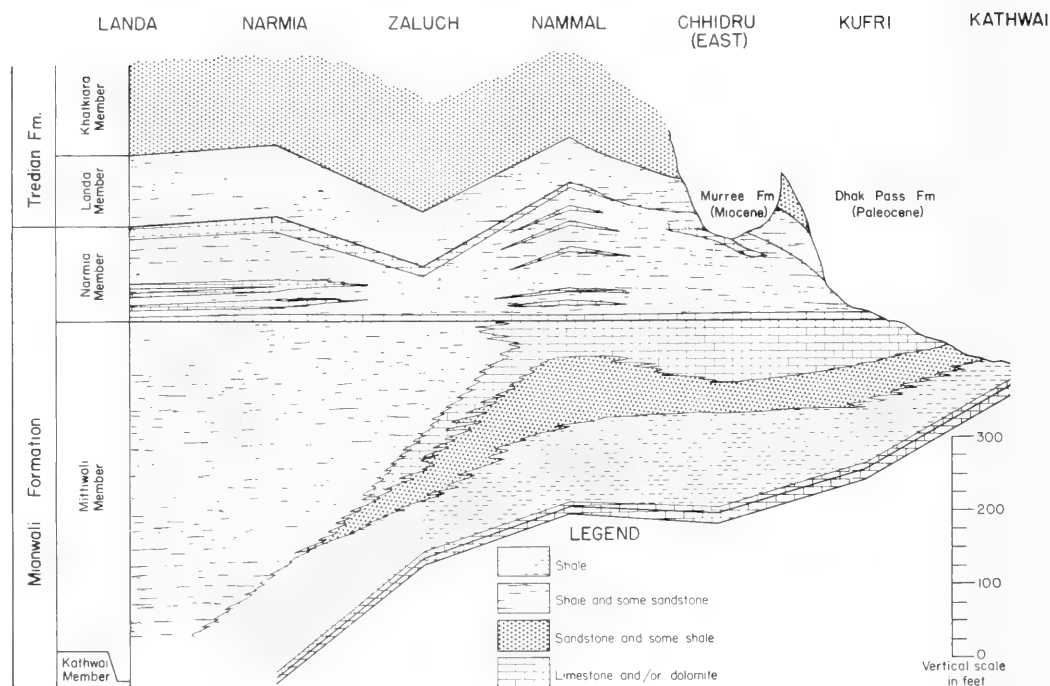
Figure 5. Diagrammatic reconstruction of facies relationships of Lower and Middle? Triassic strata in the Salt Range and Surghar Range of West Pakistan.

ammonoid zones. I have in progress an intensive revision of this fauna. Like the underlying Kathwai Member, the Lower Ceratite limestone is remarkably uniform throughout the Salt Range and the Trans-Indus Ranges.

It is in the remaining strata of the Mitti-wali Member that one finds an interesting diversity in lithofacies. Waagen's sequence of the Ceratite marls, Ceratite sandstone, and the Upper Ceratite limestone is recognizable in a general way only in the central region of the Salt Range from Nammal Gorge east to Kufri. West of Nammal Gorge this portion of the Mittiwali Member becomes a fairly homogeneous sequence of shale, silty shale, with some thin sandstone and limestone beds. A diagrammatic interpretation of these east–west facies changes is shown on Figure 5.

The Ceratite marls are clay shales, greenish to gray-black in color, with fairly numerous lenticular beds (1 to 6 inches thick) of argillaceous limestone. The Ceratite marls are very fossiliferous, but the fossils are almost entirely restricted to the thin lenticular limestone beds. The fauna is completely dominated by ammonites with a few nautiloids and pelecypods. The ammonoids are being extensively revised and will not be treated here. The most common nautiloid species is *Menuthionautilus kieslingeri* Collignon; in addition, much less common species include: *Grypoceras bidorsatoides* Kummel, *Grypoceras aemulans* Kummel, and *Pleuronautilus kokeni* Frech (Kummel, 1953). Among the pelecypods, Lukas Waagen (1900, p. 286) has identified *Pecten discites* Schlotheim and *Pecten* cf. *albertii* Goldfuss. Ostracods (I. G. Sohn, written communication) and conodonts (W. Sweet, written communication) are also present.

The Ceratite marls grade upward into

the Ceratite sandstone beds. These sand beds are massive to laminated in bedding, frequently crossbedded, and have ripple marks. The laminated units generally contain numerous thin shale laminae and are usually micaceous. The Ceratite sandstone is generally friable and soft, forming low covered slopes. This unit is well exposed only in Nammal Gorge and along the east side of Chhidru Nala. At all other localities studied in this part of the Salt Range this unit was mostly covered. The Ceratite sandstone is characterized by two very conspicuous fossils: large specimens of *Flemingites* (up to two feet in diameter) and the bellerophontid *Stachella*. Waagen (1895) considered this bellerophontid to be confined to the mid-part of his Ceratite sandstone and on this basis divided the unit into three divisions and zones. There is one outcrop of the Ceratite sandstone in the upper part of Chhidru Nala where *Stachella* does occupy this position, but in another part of the Nala, where the Ceratite sandstone crops out, *Stachella* is absent. *Stachella* was likewise not found in the Ceratite sandstone exposed in Nammal Gorge, nor at any other locality. It is highly dubious that this bellerophontid has any stratigraphic significance.

As in the other members of the Mianwali Formation, ammonites dominate the fauna; comments on the ammonoids will be reserved for a later paper. Among the non-ammonoid fossils, Lukas Waagen (1900, p. 286) identified: *Pecten discites* Schlotheim var. *microtis* Bittner, *Pseudomonotis* ex aff. *telleri* Bittner, *Pleurophorus?* (*Clidophorus?*) sp., *Nucula* sp., *Macrocheilus?* sp., *Turbonilla* (*Holopella*) *gracilior* Schauroth, *Amauropsis?* sp., *Bellerophon* (*Stachella*) sp., *Rhynchonella* sp.

The Ceratite sandstone grades upward into the Upper Ceratite limestone. The unit is somewhat misnamed as limestone comprises only about 60 per cent of the unit, the remainder consisting of shale and sandstone. Eastward at Chhidru and at Kufri, sandstone and shale comprise an even larger percentage of the unit, and much of the limestone is conspicuously sandy. The limestone is gray, thin to medium bedded, fine grained, and contains abundant fragmental shell remains. The limestone beds are generally quite fossiliferous but unfortunately the preservation is, with few exceptions, very poor. Like the lower units of the Mianwali Formation, the ammonites completely dominate the fossil faunas. In addition, there are seen occasional pelecypods but little else. The ammonite fauna includes *Anasibirites*, *Prionites*, *Hemiprionites*, etc., and is undergoing complete restudy. Lukas Waagen (1900, p. 287) identified the following pelecypods from this unit: *Gervillia* cf. *exporrecta* Lepsius, *Pecten* ex aff. *ussuricus* Bittner, *Myophoria* cf. *laevigata* Alberti, *Pecten albertii* Goldfuss, *Nucula* sp.

Narmia Member

This unit comprises the strata Waagen (1895) called the Bivalve beds, Dolomite beds and the Topmost limestone. It has been the least understood part of the "Ceratite Formation." This is mainly due to the treatment of these units by Wynne and Waagen in their publications on the Salt Range.

Throughout the Salt Range and Trans-Indus Ranges the basal bed of the Narmia Member is a thin (ten feet more or less), complex limestone. At Chhidru and Kufri this basal limestone unit is the Bivalve limestone of Waagen. It is a hard, light-gray, massive limestone, mainly a coquina of pelecypods. At Chhidru this limestone bed also contains poorly preserved ammonites and nautiloids (*Enoploceras* and orthocerids) in addition to the pelecypods. In Nammal Gorge this limestone unit is seven feet thick and consists of alternating coquinoid beds, like those that make up the whole unit at Chhidru and Kufri, and irregularly bedded limestone containing poorly preserved brachiopods, ammonites, pelecypods, and gastropods. At Zaluch Nala the unit is like that at Narmia, but in ad-

dition contains some glauconite. In the Surghar Range, at Narmia and Landa, this basal limestone unit no longer is a pelecypod coquina but is a dark-gray to brown, fragmental limestone, sandy in part, containing poorly preserved pelecypods, ammonites, and brachiopods.

Much of the remainder of the Narmia Member consists of olive to gray-black shales, often with thin laminae and beds of fine sandstone interbedded with 2 to 10 foot beds of limestone. These limestone beds are highly varied in their lithologies. They are often dolomitic, glauconitic, pelletal, sandy, and occasionally have thin shale interbeds. The uppermost unit of the Narmia Member in the Surghar Range is a unique pisolite bed containing *Spiriferina* and other brachiopods and echinoid spines. The pisolite bed is 7 feet thick at Narmia and 4.5 feet thick at Landa Nala. In the Salt Range there are much fewer limestone beds in the Narmia Member, the few hard carbonate beds which do exist are either dolomitic limestone or dolomite. At Zaluch, for instance, the uppermost beds of this member are gray to brown massive dolomite. This may also be observed in Nammal Gorge. In the Salt Range at Nammal Gorge and Zaluch the non-carbonate portion of the Narmia Member contains a much higher percentage of sand relative to shale than in the Surghar Range. At Chhidru the Narmia Member, aside from the basal "Bivalve limestone" and an upper dolomite bed, consists of tan sandstone that is micaceous and shaly in part.

The Narmia Member is 128 feet thick at Landa and 140 feet at Narmia in the Surghar Range, 75 feet at Zaluch, 189 feet at Nammal Gorge, 118.5 feet at Chhidru, and only 10 feet at Kufri. At Chhidru the member is truncated by erosion and overlain by the Miocene Murree Formation. In Khan Zaman Nala, about 1 mile east of the Chhidru Nala section, the Narmia Member is again fully developed, though its thickness has not been measured (Curt Teichert, written communication). At Kufri it is overlain by Paleocene limestone. The thinness of the member at Zaluch is believed to be due to minor faulting within the sections and has no regional significance.

The limestone beds of the Narmia Member are fossiliferous but, unfortunately, fossils are neither abundant nor well preserved. The fauna includes ammonites, nautiloids, brachiopods, echinoid spines, and crinoid remains. The most important of these fossils, at least for dating the member, are the ammonites. In the systematic portions of this report 15 species of ammonites are described; Waagen (1895) had described 4 species. This ammonite fauna clearly indicates a late Scythian age for the Narmia Member.

TREDIAN FORMATION

Immediately overlying the Mianwali Formation are a series of non-marine strata about which there has been some confusion. Gee (1947) was the first to recognize these strata and proposed the name Kingriali Sandstones for them. Subsequent work has revealed that two distinct mappable units can be recognized within the Kingriali Sandstones: a lower predominantly shale unit and an upper predominantly sandstone unit. At the time he introduced the name Kingriali Sandstones, Gee (1947) also named the overlying strata the Kingriali Dolomites. Both are presumably of Triassic age, but to avoid a double usage of the name Kingriali, the name Tredian Formation (Gee, in press, in report of Stratigraphic Commission, Geological Survey of Pakistan) was introduced (See Table 3). For the lower shaly member of the Tredian Formation I have proposed the name Landa Member, and for the upper sandy member of the formation, Danilchik and Shah (in press) have proposed the name Khatkiara Member. I have not studied the Khatkiara Member, therefore only the beds assigned to the Landa Member will be discussed here.

Landa Member

The type section of this member is in Landa Nala in the Surghar Range where it is 100 feet thick. The member consists of sandstone and shale, in about equal proportions. The sandstone may be black, pink, or red, and is micaceous, thin to massively bedded, with ripple marks and slump structures. The shale is generally black, sandy and micaceous. The member is 72 feet thick in Zaluch Nala and 63 feet in Nammal Gorge. The member is not present in Chhidru Nala but is fully developed one mile to the east in Khan Zaman Nala (Curt Teichert, written communication). East of Khan Zaman Nala the member is rapidly beveled and is not present at Kufri nor Kathwai.

The only fossils observed in the Landa Member are poorly preserved and fragmentary plant remains. The samples of fossil plants and shale reported on by Sitholey (1943), Pant (1949), and Pant and Srivastava (1964), from south of Sakesar Ridge in the Salt Range, are most probably from the Landa Member.

AGE AND CORRELATION OF MIANWALI FORMATION

It has long been established that the Ceratite beds of the Salt Range are of Lower Triassic, Scythian age. In fact they were selected by Waagen and Diener (in Mojsisovics, Waagen and Diener, 1895) as the type section of the Scythian for the "pelagischen Sedimente des Trias-Systems." Waagen's early efforts to place the Upper Ceratite limestone in the Middle Triassic and to assign his Dolomite unit to the Keuper were never accepted. Noetling (1901, 1905) interpreted the fossiliferous Triassic beds of the Salt Range (through the zone of *Stephanites superbus* of the Upper Ceratite limestone) as including a complete succession of faunal zones for the Scythian. This view was held by Diener (1912, p. 256), Welter (1922, p. 92), and others.

This view on the age span of the Ceratite beds and the scope of the Scythian stage generally prevailed until Spath (1930, p. 76) published a preliminary scheme for the subdivision of the Scythian. This scheme is shown on Table 4. This is an extremely interesting modification of the earlier attempt to establish subdivisions of the Scythian. This zonal scheme was presented within a chapter discussing the age of the East Greenland early Triassic fauna (Spath, 1930) and prior to completion of the British Museum Triassic catalogue. This discussion is sufficiently brief and ambiguous as to leave unclear the complete justification and evidence for the proposal. The sequence of zones, except that of *woodwardi,* is that adopted by Noetling (1905) for the Ceratite beds of the Salt Range. This scheme differs in detail from the proposals and conclusions of previous authors but it agreed with several of these in having a single zone (*superbus*) to represent most of the upper Scythian. At the same time, within the upper Scythian, Spath (1930, p. 76) recognized three ages—the Owenitan, Columbitan, and Stephanitan.

Spath's 1930 proposal was the first new addition to Scythian chronology for quite some time. It was admittedly a tentative scheme in need of further analysis. What was critically lacking, especially for the upper part of the scale, were sufficient stratigraphic sections with these faunal zones in sequence. Spath was cognizant that Hyatt and Smith (1905) and Smith (1914) had reported Scythian ammonoid faunas in sequence in southeastern Idaho but up until the time of Spath's 1930 paper on East Greenland these faunas had been described only in a token fashion and stratigraphic data were very limited. Smith's (1932) monograph on the Lower Triassic ammonoids of North America provided a comprehensive treatment of these ammonoid faunas with data on their stratigraphic and geographic distributions. This monograph was a posthumous publi-

TABLE 4. SUBDIVISIONS OF LOWER TRIASSIC (SCYTHIAN) PROPOSED BY SPATH (1930)

	Ages	Zones (India)	Some Equivalents
Upper	Stephanitan		*Arctoceras* beds, Spitsbergen; *Olenekites* beds, N. Siberia
	Columbitan	*superbus?*	*Columbites* beds, Albania; *Anasibirites* beds, Spitsbergen; Utah, Timor; *Tirolites* Beds, Werfen
	Owenitan		*Meekoceras* beds, California *Meekoceras* beds, Timor;
Lower	Flemingitan	*flemingianus* *volutus* *fallax*	*Hedenstroemia* beds, Himalayas (lower part) "*Ophiceras*" beds, Timor
	Gyronitan	*rotundatus* *radiosus*	"*Meekoceras*" beds, Himalayas *Proptychites* beds, Primorye
	Otoceratan	*woodwardi*	*Proptychites* beds, Greenland *Otoceras* beds, Greenland

cation as Dr. J. P. Smith passed away on January 1, 1931. In southeastern Idaho, Smith encountered within the Thaynes Formation a sequence of three ammonoid faunas which formed the basis for part of his chronologic scheme for the Lower Triassic:

Columbites Zone
Tirolites Zone   ⎰ *Anasibirites* Subzone
Meekoceras Zone ⎨ *Owenites* Subzone
                ⎪ *Pseudosageceras multilobatum*
Genodiscus Zone ⎩   Subzone
Otoceras Zone

The lower two zones—*Genodiscus* and *Otoceras*—had not been identified by Smith in western United States. The upper three zones were important for they occurred in stratigraphic superposition within the Thaynes Formation. Smith considered his *Anasibirites* Subzone to be equivalent to the fauna of the Upper Ceratite limestone of the Salt Range. Smith furthermore considered the specimen Waagen (1895, p. 130, pl. 21, figs. 1a-c) described as *Pseudharpoceras spiniger* as allied to his own species *Pseudharpoceras idahoensis* from the *Columbites* fauna of southeast Idaho and thus of *Columbites* Zone age. According to this stratigraphic scheme the Triassic formations of the Salt Range and the

Trans-Indus Ranges included a complete sequence of faunal zones except for the *Otoceras* Zone and the *Tirolites* Zone. The Lower Ceratite limestone was assigned to the *Genodiscus* Zone, the Ceratite sandstone was assigned to the *Pseudosageceras multilobatum* Subzone (the Ceratite marls are not mentioned), the Upper Ceratite limestone was assigned to the *Anasibirites* Subzone, and the beds with *Pseudharpoceras spiniger*, presumably from the Topmost limestone of the Dolomite beds, were assigned to the *Columbites* Zone. This scheme, like that of Spath (1930), resulted in an enlarging of the scope of the Scythian and at the same time reducing the presumed degree of completeness of the Salt Range formations.

Smith's zonal scheme and analysis of the Scythian came under the searching pen of L. F. Spath (1933, 1934). Though Spath was rather caustic in his remarks on Smith's zonal schemes, the differences between these two authorities were not really all that great and were more apparent than real. In 1934, in the British Museum Catalogue on Triassic Cephalopoda, Spath presented a modified and more detailed scheme for subdivisions of the Lower Triassic (Table 5). The sequence of zones

TABLE 5.   SUBDIVISIONS OF THE LOWER TRIASSIC (SCYTHIAN) PROPOSED BY SPATH (1934)

	Divisions	Zones	Equivalents
Upper Eo-trias	Prohungaritan (Olenikitan?)		Upper *Arctoceras* beds, Spitsbergen. Olenek beds, Siberia (partim). *P. middlemissi* beds, Kashmir.
	Columbitan	*Columbites* *Tirolites*	*Subcolumbites* beds, Albania, Timor. *Columbites* beds, Idaho. *Tirolites* beds, Alps, etc., Idaho.
	Owenitan	*Anasibirites*	*Anasibirites* beds, Timor, Utah. Chocolate Limestone, Byans? Upper Ceratite limestone, Salt Range. *Kashmirites* beds, Kashmir, Timor.
		Owenites *Pseudosageceras*	*Meekoceras* beds, Timor, Idaho, California. Timor, Himalayas, W. America.
	Flemingitan	*Flemingites flemingianus* *Koninckites voltus*	Ceratite sandstone, Salt Range. Upper Ceratite marl, „
	Gyronitan	"*Celtites*" *fallax* *Prionolobus rotundatus* "*Celtites*" *radiosus*	Middle Ceratite marls, Salt Range. Lower „ „ „ „ Lower Ceratite limestone, Salt Range. Primorye beds? *Proptychites* beds, E. Greenland.
Lower Eo-trias	Otoceratan	*Ophiceras tibeticum* *Episageceras dalailamae* *Otoceras woodwardi*	*Ophiceras* beds, Kashmir, E. Greenland. *Otoceras* beds, Himalayas, E. Greenland.

for the Gyronitan and Flemingitan divisions is that proposed by Noetling (1905) for the sequence of faunas in the Lower Ceratite limestone, the Ceratite marl, and the Ceratite sandstone of the Ceratite beds in the Salt Range. For the Owenitan division Spath adopted Smith's (1932) scheme for his *Meekoceras* Zone but raised the subzones to zonal rank. The Upper Ceratite limestone was correlated with the *Anasibirites* Zone. *Pseudharpoceras* was not taken into account in this scheme. It can readily be seen that this zonal scheme differs from that proposed by Smith (1932) mainly in the assumption of a division above the Columbitan of one or more zones. In this conclusion Spath was guided mainly by "intuition" supported by the biologic character of the faunas. The stratigraphic data on the faunas he assigned to his Prohungaritan division were either completely lacking or very ambiguous. In his conclusions, explaining the significance of

the Prohungaritan division, Spath (1934, p. 34) states: "I am merely relying on the obvious differences between the lowest Anisian and the highest Scythian faunas so far known, and the only difficulty is to find a name for this time interval that will prove sufficiently accurate to serve for a label, even if it is not the best that could ultimately be proposed." Spath's conclusions regarding additional zones above the *Columbites* Zone was verified with the discovery of a *Prohungarites* fauna in the Thaynes Formation of southeast Idaho 1,000 feet above the *Columbites* fauna (Kummel, 1954). This particular fauna contains faunal elements common to the *Subcolumbites* faunas of Tethys (Albania, Chios, Timor) and to the Olenek faunas that Spath included in his Prohungaritan division.

The strata included in the Mittiwali Member include zones of the Gyronitan, Flemingitan, and Owenitan divisions of

TABLE 6. SUMMARY OF NUMBER OF SPECIMENS AND NUMBER OF SPECIES RECOGNIZED BY WAAGEN (1895) IN THE TRIASSIC FORMATIONS OF THE SALT RANGE, WEST PAKISTAN

Horizon		Number of Species	Number of Specimens
Topmost limestone		1	1
Bivalve beds		3	7
Upper Ceratite limestone		37	45*
Ceratite sandstone	Upper	12	18
	Middle	21	24**
	Lower	11	17
Ceratite marls		20	44
Lower Ceratite limestone		21	38***
Unknown		12	13
	Total	138	207

* Three species Waagen stated as being represented by several specimens; these are not included here.

** One species from this horizon is listed by Waagen as being represented by several specimens and this is not included here.

*** One species from this horizon is listed by Waagen as being represented by several specimens and this is not included here.

Spath. The discovery of *Ophiceras connectens* by Schindewolf in the Kathwai Member and verified in my own field investigations, including the presence of a specimen of *Glyptophiceras*, clearly establishes the Otoceratan age of this member. It is now amply apparent that the Ceratite beds and the Upper Ceratite limestone of Waagen are not representative of the complete Scythian but at most include no more than two-thirds of that stage. The taxonomy of the ammonites from these Salt Range Triassic strata is sorely in need of revision. Of the 138 species described by Waagen in his 1895 monograph, 134 came from strata here classified as the Mittiwali Member of the Mianwali Formation. In general the Salt Range Triassic ammonites are not well preserved. Noetling (1901, p. 408) has pointed out that 99 species (approximately 70 per cent of Waagen's 138 described species) were based on a single specimen; of these half were stated to be poorly preserved and fragmentary specimens. Vredenburg (*in* Hayden, 1911, pp. 58–60) examined collections made by Noetling in

1899–1900 and made particular note of the weathered nature of many of Waagen's specimens. On Table 6 are listed the number of specimens Waagen (1895) had, and the number of species he recognized for each of his stratigraphic divisions. These data reflect well the statistics compiled by Noetling and quoted above.

My own field studies on the Kathwai and Mittiwali Members in the Salt Range and Surghar Range have yielded a very large collection of fossils. The specimens of many of these collections are of poor to moderate preservation. At the same time, a number of collections are of excellent preservation. All the type specimens of Waagen's 1895 monograph, that are still preserved, have been personally examined and photographed. In addition, the Paleontological Institute of Tübingen University and the British Museum (Natural History) have representative suites of Salt Range Triassic ammonites which have been examined. Studies of all these collections are well advanced but as yet not completed. The results to date show considerable change and revision of the systematics of these ammonoids; in addition, the zones (as recognized by Noetling [1905]) that have been accepted by most subsequent Triassic students do not reflect the actual vertical distribution of the genera and species and thus need a complete revision.

The most significant new aspect regarding the Triassic formations of the Salt Range is a clearer definition of the strata above the Upper Ceratite limestone, designated here as the Narmia Member of the Mianwali Formation. These strata have yielded a number of fragmentary and generally poorly preserved ammonites among which I have identified 15 species. Waagen (1895) described three species—*Dinarites sinuatus*, *Lecanites laqueus*, and *Lecanites planorbis*—from his "Bivalve beds" at Chhidru, and *Pseudharpoceras spiniger* from an unknown horizon (but thought to be the Topmost limestone) at Sheik-Budin Hills, in the Trans-Indus

TABLE 7.   GEOGRAPHIC DISTRIBUTION OF GENERA PRESENT IN THE NARMIA MEMBER OF THE MIANWALI FORMATION

	Albania (*Subcolumbites* fauna)	Chios (*Subcolumbites* fauna)	Mangyshlak Peninsula	Salt and Surghar ranges, West Pakistan	Timor (*Prohungarites* fauna)	Kwangsi, China (*Subcolumbites* fauna)	Primorye region (*Subcolumbites* fauna)	Olenek region (*Olenekites* fauna)	Spitsbergen (*Keyserlingites* fauna)	Ellesmere Island (*Keyserlingites* fauna)	British Columbia (Toad-Grayling Formation)	Tobin Range, Nevada (*Subcolumbites* fauna)	Confusion Range Utah	S. E. Idaho (*Prohungarites* fauna)
Pseudosageceras	x	x	x	x			x	x					x	x
Subvishnuites	x			x										
Xenoceltites				x		x	x							
Procarnites	x	x	x	x	x	x	x				x			
Isculitoides	x	x		x	x	x	x				x	x		x
Anakashmirites				x										
Svalbardiceras				x				x	x	x	x			x
Stacheites				x									x	x
Dagnoceras	x			x	x	x								
Nordophiceras				x		x		x						
Arctomeekoceras				x				x						
Tirolites	x		x	x				x					x	
Prohungarites			x	x	x			x						x

region. The ammonite fauna of the Narmia Member, described here, includes the following species:

> *Pseudosageceras multilobatum* Noetling
> *Subvishnuites* sp. indet.
> *Xenoceltites sinuatus* (Waagen)
> *Xenoceltites* sp. indet.
> *Procarnites kokeni* (Arthaber)
> *Isculitoides* sp. indet.
> *Anakashmirites* sp. indet.
> *Svalbardiceras* sp. indet.
> *Stacheites* sp. indet.
> *Dagnoceras* sp. indet.
> *Nordophiceras planorbis* (Waagen)
> *Nordophiceras* cf. *planorbis* (Waagen)
> *Arctomeekoceras* sp. indet.
> *Tirolites* sp. indet.
> *Prohungarites* cf. *crasseplicatus* (Welter)

For the purposes of clarifying the age of the Narmia Member, the species of *Procarnites*, *Stacheites*, *Arctomeekoceras*, *Isculitoides*, *Svalbardiceras*, *Dagnoceras* and *Prohungarites* are the most significant (Table 7). *Procarnites kokeni* is a prominent member of the *Subcolumbites* fauna of Albania,

Chios, and Kwangsi, China and the *Prohungarites* fauna of Timor. Closely related species occur in the *Subcolumbites* beds at Cape Zhitkov, Primorye region, Siberia (Kiparisova, 1961), and in the "Toad-Grayling" Formation of British Columbia a few feet below *Keyserlingites subrobustus* (Tozer, 1965). The Scythian formations of the Mangyshlak Peninsula have yielded one species of *Procarnites*, *P. andrusovi* (Kiparisova, 1947), which appears to be conspecific with *P. kokeni*. Astakhova (1960b) lists *P. andrusovi* as occurring in her *Pseudosageceras* Zone which she correlated with the *Flemingites* beds of the Primorye region, the *Pseudosageceras* beds of North America, and *Pseudosageceras* and *Flemingites* beds of Timor. The only other species Astakhova lists as occurring with *Procarnites andrusovi* is *Pseudosageceras multilobatum*, a species that ranges throughout the Scythian. There is no basis whatsoever for the correlation she recom-

mends; it is more likely that the greater part of the Mangyshlak sequence is of late Scythian *Prohungarites* Zone age. At least the Mangyshlak occurrence needs thorough checking. All other records of *Procarnites* and especially *Procarnites kokeni*, place it with *Subcolumbites* or *Prohungarites*.

The single specimen assigned to *Dagnoceras* is very similar to *Dagnoceras zappanense* from the *Subcolumbites* beds of Albania and the *Prohungarites* fauna of Timor. Related species are known from late Scythian horizons in Kwangsi, associated with *Hellenites*. *Isculitoides* is another genus common in late Scythian faunas. Species of this genus are known from the *Subcolumbites* faunas of Albania and Chios, the *Prohungarites* fauna of Timor, from Kwangsi, China associated with *Procarnites* and *Proptychitoides*, the *Subcolumbites* beds of the Primorye region, the "Toad-Grayling" Formation of British Columbia, the Tobin Formation of Nevada associated with *Subcolumbites*, and the Upper Thaynes Formation of southeastern Idaho associated with *Prohungarites* and *Keyserlingites*.

Svalbardiceras is known mainly from Arctic localities. It is present, associated with *Keyserlingites*, in the Olenek fauna of Siberia, in Spitsbergen, and in British Columbia. It is known from Ellesmere Island in association with *Olenekites*, and southeastern Idaho with *Keyserlingites* and *Prohungarites*. A single species of *Svalbardiceras* is known from the *Columbites* fauna of southeastern Idaho.

The form of *Prohungarites* recorded from the Narmia Member is very similar to the species listed as *Prohungarites* cf. *crasseplicatus* recorded from the Upper Thaynes Formation of southeastern Idaho (Kummel, 1954). Both the Salt Range and Idaho forms are, however, specifically distinct from the Timor *Prohungarites crasseplicatus*. The specimens assigned to *Arctomeekoceras* sp. indet. are the most abundant form in the Narmia fauna. They are most comparable to *Arctomeekoceras rotundatum* of the Olenek fauna on the

Siberian coastal region. *Stacheites* was established for a species in the Werfen fauna of Muć, Dalmatia. In recent years several new species of the genus have been described, all from late Scythian faunas. The genus is represented in the *Subcolumbites* faunas of the Tobin Formation of Nevada. The genotype is also present in the highest Scythian faunal zone of the Mangyshlak Peninsula, associated with *Arnautoceltites* and *Leiophyllites* (Astakhova, 1960b).

Subvishnuites, *Xenoceltites*, and *Anakashmirites* are known mainly from mid-Scythian faunas. Their presence in the Narmia Member extends the range of these genera considerably. *Nordophiceras* was first described from the *Dieneroceras* Zone of Popov (1961) for the Siberian region. It is a very common form in the *Columbites* fauna of southeastern Idaho, a fauna I believe to be equivalent to that of the *Dieneroceras* Zone of Siberia. *Pseudosageceras multilobatum* is probably the most common and widespread species of Scythian ammonoids; it has no zonal significance except to mark the Scythian stage. *Tirolites* is mainly known as the principal element of the Werfen fauna of the Alpine region which is placed just below the *Columbites* Zone in our sequence of Scythian zones. The genus, however, is represented in the *Columbites* fauna of Idaho, in the *Subcolumbites* fauna of Albania, in late Scythian strata of northern Siberia, and in a late Scythian fauna in the Confusion Range of Utah (Silberling *in* Hose and Repenning, 1959, p. 2188).

Finally, there is the specimen Waagen (1895, p. 130, pl. 21, figs. 1a, b, c) described as *Pseudharpoceras spiniger*. This specimen was collected by Dr. Verchere in the Sheik-Budin area at Paniala Black Hills in the Trans-Indus region. The horizon was indicated as a yellow limestone at the base of the Variegated (Jura-Rhaetic) Series at the top of the Ceratite Formation. Waagen (1892a, b) concluded that this was the Topmost limestone unit of his

Dolomite group. The uncertainty of the horizon from which this specimen was collected has created differences of opinion by subsequent workers on the Salt Range Triassic. Noetling (1901, p. 406) was skeptical that the specimen actually came from the Triassic strata but since it did not come from the Salt Range he merely shrugged off the problem as without solution and did not mention it again in his later writings. Smith (1932, p. 81) accepted Waagen's genus "however unsatisfactorily founded and described" and described a new species, *Pseudharpoceras idahoense* from the *Columbites* fauna of southeastern Idaho. Smith also believed that *Tropiceltites praematurus* Arthaber (1911) from Albania "evidently belongs to *Pseudharpoceras*." In the first part of his Triassic catalogue, Spath (1934) mentions *Pseudharpoceras* only briefly. However, in the second part of his catalogue (Spath, 1951, p. 9) he concluded "the genus *Pseudharpoceras* may safely be rejected" because of its poor preservation and the uncertainty of its stratigraphic position. On rejection of Waagen's genus, he (Spath) accepted Smith's Idaho species and introduced a new generic name for it, *Pseudarniotites*. The rich and varied late Scythian fauna from Chios described by Renz and Renz (1948) contains a large representation of the forms Arthaber had assigned to *Tropiceltites*, for which Renz and Renz introduced the genus *Hellenites*. The species Smith (1932) described from the *Columbites* fauna is congeneric with these Albanian and Chios species of *Hellenites*, thus making *Pseudarniotites* a synonym (Kummel, *in* Arkell et al., 1957, p. L149).

Waagen's type specimen is not in the collections of the Geological Survey of India and is apparently lost. There is, however, a mold of a part of one side of the specimen and this is illustrated on Plate 4, figure 7, and a cast of this mold is shown on Plate 4, figure 6. Unfortunately, the mold has no trace of the venter. It can readily be seen that Waagen's illustrations

of this species (1895, pl. 21, fig. 1) are highly restored. The morphological features that can be observed on the specimen and interpreted from Waagen's description show a close relationship to the Albanian and Chios species placed in *Hellenites* and to the Idaho species that Smith (1932) placed in *Pseudharpoceras*. However, because that all that remains is a partial mold of the poorly preserved only specimen, and because the stratigraphic horizon of the specimen is in doubt, I agree with Spath that the genus and species had best be suppressed.

The assemblage of species in the Narmia Member is considered to be of late Scythian age encompassing the Prohungaritan division of Spath (Table 5). Late Scythian faunas are now known from Albania, Chios, the Mangyshlak Peninsula, West Pakistan, Kashmir, Timor, New Zealand, China, Japan, Primorye region, northern Siberia, Spitsbergen, Ellesmere Island, British Columbia, Nevada, and Idaho. These late Scythian faunas are large and diverse, including 59 genera. A complete taxonomic revision of all these faunas [by me] is nearing completion. One of the conclusions of that study is that there is only one zone of Scythian ammonoids above the *Columbites* Zone. There are regional faunal differences, but these I do not believe reflect any significant time difference, but rather to be due to biological, lithofacies, geographic factors, and to factors of preservation. One handicap in the interpretation is the lack of stratigraphic data for many of these faunas. For instance, the Albanian, Chios, Timor, Japanese, New Zealand, and Nevada (Tobin Formation) faunas are stratigraphically isolated with neither younger nor older faunas in known sequence. Fairly good stratigraphic data are available for most of the other localities listed above. Six of the genera of the Narmia fauna (*Procarnites, Isculitoides, Svalbardiceras, Dagnoceras, Arctomeekoceras,* and *Prohungarites*) are restricted to horizons containing *Subcolumbites, Prohungarites, Keyser*-

lingites, etc. Three of the genera (*Stacheites, Nordophiceras,* and *Tirolites*) occur in some of these late Scythian faunas but also occur in the underlying *Columbites* or *Tirolites* zones. The remaining genera are more long ranging forms.

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SYSTEMATIC PALEONTOLOGY

Class CEPHALOPODA Cuvier, 1797
Subclass AMMONOIDEA Zittel, 1884
Family SAGECERATIDAE Hyatt, 1900
Genus *Pseudosageceras* Diener, 1895
Type species, *Pseudosageceras multilobatum*
    Noetling, 1905

Pseudosageceras multilobatum
    Noetling, 1905
    Plate 1, figures 11, 12

Pseudosageceras multilobatum Noetling, 1905, p. 181, pls. 19–27; Frech, 1905, pl. 23, figs. 4, 5, pl. 25, fig. 1, pl. 26, fig. 3; Krafft and Diener, 1909, p. 145, pl. 21, fig. 5; Wanner, 1911, p. 181, pl. 7, fig. 4; Diener, 1915, p. 237; Diener, 1917, p. 173, pl. 1, fig. 13; Welter, 1922, p. 94, fig. 3; Diener, 1925, p. 96, fig. 26; Smith, 1932, p. 87, pl. 4, figs. 1–3, pl. 5, figs. 1–6, pl. 25, figs. 7–16, pl. 60, fig. 32, pl. 63, figs. 1–6; Kutassy, 1933, p. 630; Collignon, 1933, p. 24, pl. 11, fig. 2; Spath, 1934, p. 54, fig. 6a; Kiparisova, 1947, p. 127, pl. 25, figs. 3–4; Kummel, 1954, pp. 185–187; Chao, 1959, p. 183, pl. 1, figs. 9, 12; Silberling, *in* Hose and Repenning, 1959, p. 2194; Astakhova, 1960b, p. 149; Tozer, 1961, p. 44, pl. 13, figs. 8, 9; Astakhova, 1962, p. 75.
Pseudosageceras intermontanum Hyatt and Smith, 1905, p. 99, pl. 4, figs. 1–3, pl. 5, figs. 1–6, pl. 63, figs. 1, 2; Mathews, 1929, p. 3, pl. 1, figs. 18–22; Renz, 1945, p. 301; Renz, 1947, p. 175; Renz and Renz, 1947, p. 62; Renz and Renz, 1948, p. 90, pl. 16, figs. 4, 7.
Pseudosageceras multilobatum var. *giganteum* Kiparisova, 1947, p. 127, pl. 26, figs. 2–5; Popov, 1961, p. 13, pl. 2, figs. 1, 2.
Pseudosageceras cf. *multilobatum,* -Kiparisova, 1961, p. 30, fig. 3.
Pseudosageceras schamarense Kiparisova, 1961, p. 31, pl. 7, figs. 3, 4.

Five fragmentary specimens of poor to fair preservation are in the collection. It is the characteristic shape of the conch and the suture that allows the identification.

This species is the longest ranging of any Scythian ammonoid and is present prac-tically everywhere that Scythian deposits occur. It apparently has not been recorded as yet from the lowest Scythian *Otoceras* Zone, but is present throughout the remainder of the Scythian. In the Salt Range it is well represented in the Mittiwali Member (Lower Ceratite limestone and the Ceratite marls) of the Mianwali Formation.

Occurrence. All five specimens recorded here are from the Narmia Member of the Mianwali Formation. Three specimens are from Landa Nala in the Surghar Range, one from a 3.5 foot bed of limestone 20 feet above the base of the member (bed no. 5) another from a 7 foot limestone bed 40 feet above the base of the member (bed no. 9), and the last 18 inches above the basal limestone of the Narmia Member, Mianwali Formation (bed no. 2). The fourth specimen came from a 5 foot bed of limestone in Narmia Nala, 38 feet above the base of the Narmia Member (bed no. 32). The fifth specimen came from an 8 foot bed of limestone in Nammal Gorge 126 feet above the base of the Narmia Member (bed no. 34).

Repository. Figured specimens (Pl. 1, figs. 11, 12) MCZ 9578; unfigured specimens from bed no. 2 in Landa Nala MCZ 9580, from bed no. 5 in Landa Nala MCZ 9576, from bed no. 9 in Landa Nala MCZ 9577, from bed no. 34 in Nammal Gorge MCZ 9579.

Family DIENEROCERATIDAE Kummel, 1952
Genus *Subvishnuites* Spath, 1930
Type species, *Subvishnuites welteri* Spath, 1930

Subvishnuites sp. indet.
    Plate 3, figures 1–5

Three horizons in the Narmia Member yielded seven fragmentary and/or highly weathered specimens that can be assigned to this genus on the basis of their sharp venter. The better preserved specimens are merely small fragments of phragmocone. There are two more or less complete specimens, though badly weathered, that do show the evolute nature of the conch; likewise, it is almost certain that the inner

whorls, as the later ones, are devoid of any ornamentation. The suture is shown on Figure 22J.

The type-species of *Subvishnuites*, *Vishnuites* sp. Welter (1922, p. 137, pl. 147, figs. 3–5 = *Subvishnuites welteri* Spath, 1930, p. 30), was based on a single specimen from the *Owenites* fauna of Timor. Conspecific forms have been described by Kummel (1959, p. 443, fig. 7) from an *Owenites* fauna in South Island, New Zealand, by Popov (1962b, p. 43, pl. 6, fig. 3—as *Parinyoites mastykensis*) from an *Owenites* fauna of the Caucasus Mountains, and by Kummel and Erben (1966) from an *Owenites* fauna in Afghanistan. *Subvishnuites tientungensis* Chao (1959) from the *Owenites* Zone of Kwangsi, China, is a valid species of this genus, quite distinct from S. *welteri*. I have in manuscript the description of a species from the *Columbites* fauna of southeastern Idaho. *Inyoites eiekitensis* Popov (1962a) I believe to be a species of *Subvishnuites*. It is said to come from the *Dieneroceras* Zone of Siberia, which Popov considered as equivalent to the *Anasibirites* Zone, but the associated species suggest a correlation with the *Columbites* Zone of southeastern Idaho.

All of these species and records of *Subvishnuites* are based on one or very few specimens; there is obviously a great deal yet to be learned about this generic group. The Pakistan specimens are too poorly preserved to make any meaningful comparisons with the known species of the genus. My specimens exhibit the basic morphological characters of the genus. It should be emphasized that they are the youngest specimens of the genus recorded to date.

Occurrence. Narmia Member of Mianwali Formation from: (1) a 3.5 foot bed of limestone 20 feet above the base of the Narmia Member (bed no. 5) in Landa Nala, Surghar Range; (2) a 7 foot bed of limestone 29 feet above the base of the Narmia Member (bed no. 7) in Landa Nala, Surghar Range; (3) bed 30, 32, and 36, all limestone units 17, 38, and 76 feet,

respectively, above the base of the Narmia Member, Narmia Nala, Surghar Range, West Pakistan.

Repository. Figured specimens (Pl. 3, fig. 1) MCZ 9596, (Pl. 3, figs. 2, 3) MCZ 9597, (Pl. 3, figs. 4, 5) MCZ 9598; suture specimen MCZ 9599; unfigured specimens from Landa Nala MCZ 9610; unfigured specimens from Narmia Nala MCZ 9600, MCZ 9602.

Family XENOCELTITIDAE Spath, 1930
Genus Xenoceltites Spath, 1930
Type species, *Xenoceltites subevolutus* Spath, 1930

Xenoceltites sinuatus (Waagen), 1895
Plate 1, figures 1–8

Dinarites sinuatus Waagen, 1895, p. 33, pl. 10, fig. 4; Diener, 1915, p. 122.
Xenoceltites sinuatus, -Chao, 1959, p. 194.
Lecanites laqueus Waagen, 1895, p. 285, pl. 38, figs. 9, 10.
Xenodiscus laqueus, -Diener, 1915, p. 313.

Waagen (1895, p. 33) established this species on a weathered, one-third volution of body chamber (Pl. 1, figs. 1, 2). Waagen's original illustrations of this species are fairly accurate but he included a portion of a penultimate whorl which at least at present is not part of the specimen. My own collections contain two specimens collected from the same bed and at the same locality as Waagen's type. The specimens are in a friable sandstone and in their preservation leave much to be desired. The best of the two specimens (Pl. 1, figs. 3, 4) consists of one-third volution of phragmocone; the other specimen is more complete and shows the inner whorls, but the preservation in general is very poor. *Lecanites laqueus* was established by Waagen on the basis of two very poorly preserved and fragmentary specimens (Pl. 1, figs. 5–8). They were collected from the same beds and the same locality as the type of X. *sinuatus*. There is no question but they are conspecific with the type of X. *sinuatus*.

The key feature of this species is the evolute conch with compressed elliptical

whorls. The whorl sides bear prominent, slightly forwardly projecting ribs; the venter is smooth. The suture, which was unknown to Waagen, is well developed on my illustrated specimen and is reproduced here on Figure 22H.

Xenoceltites is represented by a diverse and geographically widespread group of species in the mid-Scythian; in the upper Scythian, however, few species (or even specimens) have been recorded. The classic upper Scythian faunas of Albania, Chios, and Timor have no species of *Xenoceltites* nor are any known as yet from western North America. Species of *Xenoceltites* in late Scythian deposits are known from Utah (Silberling, *in* Hose and Repenning, 1959), Kwangsi, China, and two regions in Siberia, but none of these are morphologically particularly close to *X. sinuatus*. The species (or specimen) that shows the greatest similarity to *X. sinuatus* is *X. spitsbergensis* Spath (1934, pl. 9, figs. 2a, b) from the *Arctoceras* (= *Owenites*) beds of Spitsbergen, presumably a much older species.

The Kwangsi species, *Xenoceltites crenoventrosus* Chao (1959, p. 194, pl. 3, figs. 14–15; pl. 42, figs. 2–6), comes from beds containing a typical *Subcolumbites* fauna. Its suture is quite similar to *X. sinuatus* but the rib pattern is quite distinct. Kiparisova (1961, p. 50) assigned a few small specimens from the *Subcolumbites* beds of the Primorye region to *Xenoceltites spitsbergensis* Spath. I am willing to accept the assignment of these forms to *Xenoceltites*, but have serious doubts on the species relationships. These Primorye forms, at least, have no similarity to *X. sinuatus*. Finally, I believe the Olenek fauna contains *Xenoceltites*, namely the whole group of species Mojsisovics (1886) placed in his group "obsoleti" (Kummel, 1961, p. 521). This includes *Ceratites multiplicatus, C. hyperboreus, C. fissiplicatus,* and *C. discretus,* all new species described by Mojsisovics in his 1886 monograph on the Olenek fauna. Some of these forms (e.g., *Ceratites multiplicatus* Mojsisovics, 1886, pl. 9, figs. 15a, b) are

quite similar in many aspects to *X. sinuatus*.

Occurrence. Waagen's type specimens and the two specimens recorded here came from sandstone beds of the Narmia Member above the hard "Bivalve limestone" on the east side of Chhidru Nala, Salt Range, West Pakistan.

Repository. Holotype (Pl. 1, figs. 1, 2) GSI 7110; syntypes *Lecanites laqueus* (Pl. 1, figs. 5–8) GSI 7221, 7222; topotype (Pl. 1, figs. 3, 4) MCZ 9581; unfigured specimen MCZ 9582.

Xenoceltites sp. indet.
Plate 1, figures 9, 10

A fragmentary specimen consisting of slightly more than one-third volution of living chamber. The whorls are compressed, venter rounded, flanks only slightly convex. Whorls marked by slightly forward projecting grooves which cross the venter. The specimen is possibly conspecific with *Xenoceltites sinuatus* (Waagen), but the differences which are apparent in light of the fragmentary record of both suggest that separate treatment of this form at this time is warranted.

Occurrence. From 10 foot bed of limestone 17 feet above base of Narmia Member (bed no. 30) of the Mianwali Formation in Narmia Nala, Surghar Range, West Pakistan.

Repository. MCZ 9583.

Family PROPTYCHITIDAE Waagen, 1895
Genus *Procarnites* Arthaber, 1911
Type species, *Parapopanoceras kokeni* Arthaber, 1908

Procarnites kokeni (Arthaber), 1908
Plate 2, figures 10–13

Parapopanoceras kokeni Arthaber, 1908, p. 259, pl. 11(1), figs. 1a–c, 2a, b.
Hedenstroemia sp. Arthaber, 1908, p. 284, pl. 3, fig. 2.
Procarnites kokeni, -Arthaber, 1911, p. 215, pl. 17(1), figs. 16, 17, pl. 18(2), figs. 1–5; Diener, 1915, p. 228; Diener, 1917, p. 167; C. Renz, 1928, p. 155; Renz and Renz, 1947, p. 61; Renz and Renz, 1948, p. 81, pl. 8, figs. 5, 6–6a, 7–7a, 8–8a, 9–9a, pl. 9, figs. 2–2a.
Procarnites kokeni var. *evoluta* Renz and Renz,

1947, p. 61; Renz and Renz, 1948, p. 82, pl. 9, figs. 1–1a.

Procarnites kokeni var. *panteleimonensis* Renz and Renz, 1947, p. 61, 78; Renz and Renz, 1948, p. 82, pl. 8, figs. 3–3a, pl. 9, figs. 3–3a.

Procarnites acutus Spath, 1934, p. 183, pl. 5, figs. 4a, b (= *Hedenstroemia* sp. Arthaber, 1908, p. 284, pl. 3, fig. 2); Chao, 1959, p. 89, 255, pl. 32, figs. 8–9, pl. 33, figs. 1–8.

Procarnites skanderbegis Arthaber, 1911, p. 216, pl. 18(2), figs. 6, 7; Diener, 1915, p. 229; C. Renz, 1928, p. 155; Renz and Renz, 1947, p. 61; Renz and Renz, 1948, p. 82, pl. 8, figs. 4–4a.

Procarnites andrusovi Kiparisova, 1947 (Bajarunas, 1937, *nom. nud.*), p. 132, pl. 28, figs. 2–4, text-figs. 11–13; Astakhova, 1960b, p. 149.

Procarnites oxynostus Chao, 1959, p. 88, 254, pl. 32, figs. 1–7, 10–12, text-fig. 28a–d.

The lower part of the Narmia Member at its type locality in Narmia Nala has yielded three small specimens of this very diagnostic species. The most complete specimen (Pl. 2, figs. 10, 11) measures 23.2 mm in diameter, 8.6 mm for the width of the whorl, 11.6 mm for the height of the whorl, and 3.5 mm for the diameter of the umbilicus. The specimen which yielded the suture (Fig. 22I) consists of one-half volution of approximately 27 mm in diameter. The third specimen is a small fragment of phragmocone of only five septa. All the specimens are phragmocones.

A comprehensive review of the genus *Procarnites*, and all the species that have been assigned to it has been completed for a broad review of all Scythian ammonoids. Only a summary of this review need be given here to clarify the identity and biological affinities of the specimens recorded here.

The two syntypes of *Procarnites kokeni* (Arthaber) are small, immature specimens. Only one side of either of these specimens is preserved. Noteworthy of the smaller of these two specimens are the broadly arched lateral areas and the round umbilical shoulders; the other specimen (the paralectotype) has broader lateral areas and abruptly rounded umbilical shoulders and nearly vertical umbilical walls. These two syntypes of Arthaber's are comparable in size to the two most complete specimens

recorded here. In the shape of the whorl, nature of the venter, umbilical diameter. etc., the Salt Range specimens are nearly identical to the two Albanian primary types. The suture (Fig. 22I) likewise is very similar. As with most of the specimens from the *Subcolumbites* fauna of Albania the suture can be exposed only by grinding and polishing. This has been done on Arthaber's two type specimens, and in the process details of the denticulation patterns of the lobes are, of course, obliterated. The basic pattern of the suture of the Salt Range specimens is identical to that of the Albanian specimens, and the small differences which are present fall within the range of what can be expected as intra-specific variation.

In his monograph on the Kčira, Albania fauna, Arthaber (1911) stated he had 45 specimens for study and he illustrated six of these. Unfortunately, only three of the illustrated specimens are still available. In addition to *Procarnites kokeni*, Arthaber (1911) recognized one additional species, *P. skanderbegis*. For this species he records eight specimens of which the two illustrated syntypes are available. This species was differentiated on the basis of suture, degree of conch inflation, and ornamentation. In regards to the suture, it was the absence of minor adventitious elements in the ventral lobe to which Arthaber pointed. The modification and development of the suture in the ventral region progressively changes with growth, and on comparing the suture of *P. skanderbegis* with that of *P. kokeni* it is seen that they differ in only the smallest details.

Assessment of the significance of conch shape and ornamentation was not possible until the discovery of the *Subcolumbites* fauna of Chios which yielded a large number of specimens of *Procarnites*. A plot of the measurements of the Chios specimens assigned by Renz and Renz (1948) readily shows that no distinction can be made between these two species on the basis of whorl height or umbilical diameter. In respect to whorl width, the specimens as-

signed to *P. skanderbegis* tend to be thicker, but there is complete gradation with the more compressed forms which had been placed in *P. kokeni*.

The ornamentation of the larger of Arthaber's two syntypes consists of very faint radial folds and slightly accentuated growth lines every millimeter or so. The specimen is not well preserved, so the complete pattern of this ornamentation is not known. The smaller syntype does not show any ornamentation. None of the specimens from Chios assigned by Renz and Renz to *P. skanderbegis* show any ornamentation. Two specimens of *P. kokeni* (Renz and Renz, 1948, pl. 8, figs. 3, 5, pl. 9, fig. 3) show faint radial ribs or falcoid ribs. The poor state of preservation of the Albanian and Chios *Subcolumbites* fauna is an important factor which does not allow full evaluation of the nature and variation of the ornamentation patterns. On the basis of the data available, ornamentation does not appear to be a criterion which can be used in this case for species discrimination. Thus the criteria used to distinguish *P. skanderbegis* from *P. kokeni* do not stand up on close examination.

Spath (1934, p. 183) separated one of Arthaber's varieties of *Procarnites kokeni* as a new species—*P. acutus*. The distinction was made on the basis of an acute to oxynote venter. He (Spath) also mentions a form which he considered transitional with *P. kokeni* from the same Albanian *Subcolumbites* fauna. Examination of the large number of specimens of *P. kokeni* from Chios clearly shows complete gradation from forms with acute venters like Spath's holotype of *P. acutus* (Spath, 1934, pl. 5, figs. 4a, b) to forms with broadly rounded venters.

Procarnites andrusovi (Kiparisova, 1947) from the Mangyshlak Peninsula of the Caspian region appears to be conspecific with *P. kokeni*. Kiparisova distinguished her species on the basis of the greater width of the umbilicus and the addition of an adventive element in the ventral lobe. The umbilical width of *P. andrusovi* falls well within the variability in this feature in the population of *P. kokeni* from Chios. Variation in the ventral lobe is a function of ontogeny. Unfortunately, the stratigraphic relations of the Mangyshlak Scythian ammonoids described to date are not well known. The data given by Bajarunas (1936) and Kiparisova (1947) are ambiguous. The recent description of several species of Scythian ammonoids from Mangyshlak by Astakhova (1960a) did not include any discussion of *P. andrusovi*, but, in two stratigraphic papers, Astakhova (1960b, 1962) lists this species as part of her *Pseudosageceras* fauna that she thought to be of Owenitan age.

Chao (1959) recognized two species of *Procarnites* from Kwangsi, China. He had four specimens he assigned to *P. acutus* Spath and six specimens for which he erected a new species, *P. oxynostus*. From the measurements of the basic conch parameters given by Chao, it is readily seen that these forms are very much like the population of *P. kokeni* from Chios. In terms of whorl width they are clearly of the compressed variety, but yet fall within the range of variation of this feature as exhibited in the population from Chios. The minor differences in the suture, pointed to by Chao, are more likely expressions of poor preservation than of any real genetic significance.

The second species of *Procarnites* which I recognize is *P. immaturus* (Kiparisova, 1947, p. 130). This species is from the *Subcolumbites* beds of Cape Zhitkov, Primorye region, Siberia. It is very similar to *P. kokeni* but is distinguished on the basis of faint radial constrictions. *Procarnites modestus* Tozer (1965), from an upper Scythian horizon in the Toad Formation of British Columbia, I believe to be a synonym of the Primorye *P. immaturus* Kiparisova.

Occurrence. The three small specimens recorded here came from the lower part of the Narmia Member of the Mianwali Formation (17 feet above the base of the

member, bed no. 30) in Narmia Nala, Surghar Range, West Pakistan.

Repository. MCZ 9593 (Pl. 2, figs. 10, 11), MCZ 9594 (Pl. 2, figs. 12, 13), MCZ 9595 (suture specimen, Fig. 22I).

Family PARANANNITIDAE Spath, 1930
Genus *Isculitoides* Spath, 1930
Type species, *Isculites originis* Arthaber, 1911

Isculitoides sp. indet.

The collections include four weathered and very poorly preserved specimens. They are very involute, globular, forms, with what appears to be a very small, excentric umbilicus. The suture is visible only in vague segments; these suggest a simple ventral lobe and a single lateral lobe. The assignment of these specimens to this genus is coupled with the conclusion that the Narmia Member is of late Scythian age; there is no other genus of this age with these morphological characters.

Isculitoides is a very characteristic and widespread genus of upper Scythian ammonoids. The type species, *I. originis* (Arthaber), is present in the *Subcolumbites* fauna of Albania and Chios and in the *Albanites-Prohungarites* fauna of Timor. In Kwangsi, China, Chao (1959) has recorded *I. ellipticus* from loose blocks which also contained *Procarnites* and *Proptychitoides*, suggesting the late Scythian *Subcolumbites* age. The specimens Kiparisova (1961) described as *Paranannites suboviformis* from the *Subcolumbites* beds of the Primorye region are more correctly assigned to *Isculitoides.* Tozer (1965) has described *I. minor* from late Scythian strata (associated with *Keyserlingites, Svalbardiceras,* etc.) from northeastern British Columbia. I have descriptions of two new species, in manuscript, from western United States. One is in the Toad Formation of Nevada, associated with *Subcolumbites,* and the other in the Thaynes Formation associated with *Keyserlingites* and *Prohungarites.*

Small, globular, tightly involute forms such as *Isculitoides* are very difficult to analyze unless large populations of fairly good preservation are available. Most of the species recognized to date are known from relatively few specimens. The only large population of a species of this genus known to the writer is that of *I. originis* from the *Subcolumbites* fauna of Chios. Analysis of this population shows a very great range in variation in practically all conch parameters. It is highly possible that at least some of the species mentioned above are actually synonyms of *I. originis.* The stratigraphic range of the genus appears to be restricted to the uppermost Scythian *Subcolumbites-Prohungarites* Zone.

Occurrence. The four specimens came from a two foot bed of limestone 76 feet above the base of the Narmia Member (bed no. 36) of the Mianwali Formation, Narmia Nala, West Pakistan.

Repository. MCZ 9616.

Family KASHMIRITIDAE Spath, 1930
Genus *Anakashmirites* Spath, 1930
Type species, *Danubites nivalis* Diener, 1897

Anakashmirites sp. indet.
Plate 3, figures 6–8

The Narmia Member at Landa and Narmia Nala in the Surghar Range has yielded a number of fragments of phragmocones of a very evolute species. The whorls are oval, compressed, and bear blunt widely spaced ribs that enlarge toward the ventral shoulder. Most of the specimens appear to be crushed to a greater or lesser extent. None of the specimens are complete enough to yield any significant measurements. The suture is shown on Figure 22F.

Evolute ammonoids with radial ribs are fairly common through most of the Scythian. The taxonomy of these forms, however, is in a most unsatisfactory state. Of the several genera of these forms, the type of *Anakashmirites* and related species are most similar to the Pakistan specimens recorded here. Most of the generally accepted species of *Anakashmirites* are known from the *Owenites* Zone.

In none of the classic uppermost Scythian faunas of Albania, Chios, Timor, Kwangsi, Primorye region, northern Siberia, or western United States are there species that could be considered "typical" *Anakashmirites*. The basic form of the whorl section and ribbing pattern is similar to several species of *Anakashmirites* from the mid-Scythian *Owenites* Zone, but the suture is distinctly more advanced. Under the circumstances, we can consider this identification as merely tentative; at the moment there is no other logical group that would include these forms.

Occurrence. Narmia Member of Mianwali Formation from (1) a 7 foot bed of limestone 40 feet above the base of the Narmia Member (bed no. 9) in Landa Nala, and (2) a 10 foot bed of limestone 17 feet above the base of the Narmia Member (bed no. 30) in Narmia Nala, Surghar Range, West Pakistan.

Repository. Figured specimens (Pl. 3, figs. 6, 7) MCZ 9603, (Pl. 3, fig. 8) MCZ 9604; unfigured specimens from Landa Nala MCZ 9601, unfigured specimens from Narmia Nala MCZ 9608.

Family MEEKOCERATIDAE Waagen, 1895
Genus *Svalbardiceras* Frebold, 1930
Type species, *Lecanites* (?) *spitzbergensis* Frebold, 1929b

Svalbardiceras sp. indet.
    Plate 2, figures 6–9

This genus is recognized on the basis of a nearly complete phragmocone of only fair preservation, and a fragment of another. The more complete specimen measures 29 mm in diameter, 6.2 mm for the width of the adoral whorl, 11.8 mm for the height, and 9 mm for the diameter of the umbilicus. The whorls are compressed, broadly convex. The venter is flat and aligned by subangular ventral shoulders. The umbilical shoulders are rounded with a low but steep umbilical wall. No shell is preserved but the adoral half volution bears faint, low, radial ribs. The inner whorls, at a diameter of 5.5 mm are well preserved; at this stage

the venter is rounded, the whorls are approximately as wide as high and bear periodic constrictions across the whorl sides and venter. In addition, there are blunt nodes on the flanks. The suture is shown on Figure 22G.

The genus *Svalbardiceras* has been plagued by confusion since its introduction by Frebold (1930). That author quite clearly indicated *Lecanites* (?) *spitzbergensis* Frebold (1929b, p. 299, pl. 1, fig. 1) as the type; nevertheless, Spath (1934, p. 251) listed *Svalbardiceras spitzbergense* Frebold (1930, p. 24, pl. 4, figs. 1, 12) as lectotype. Unfortunately, the specimen described by Frebold in 1929b was destroyed in the great fire of 1943 that burned out Hamburg. The type specimen came from an horizon separate and above the *Arctoceras* beds near Agardhbay, west Spitsbergen. In the same year, Frebold described two specimens from Kap Thordsen in Eisfjord, west Spitsbergen, as *Ammonites* sp. indet. (Frebold, 1929a, p. 13, 14, pl. 1, figs. 12, 13) which he thought to be similar to his *Lecanites* (?) *spitzbergensis*. I believe these specimens to be conspecific to the type specimen from Agardhbay. The Kap Thordsen specimens are associated with *Keyserlingites*. In the next year, Frebold (1930) illustrated three additional examples of *Svalbardiceras spitzbergensis* and brought out again its stratigraphic position as being above the *Arctoceras* fauna. Frebold (1930, p. 25) states his species was found in his Grippia beds and the lower part of the Saurian beds, both of which he considered of Anisian age, a conclusion he reaffirmed in 1951. However, Tozer (1961, p. 32) quotes a personal communication from Frebold on the association of *Svalbardiceras spitzbergensis* and *Beyrichites affinis* in the lower Saurian beds as follows: "Dr. Frebold informed the writer (personal communication) that he was never completely satisfied that *Svalbardiceras* occurs with *Beyrichites affinis*. In the sections that he examined (Frebold, 1931) no such association was apparent." It is quite apparent that *Sval-*

bardiceras spitzbergensis is widespread in Spitsbergen and its association with *Keyserlingites subrobustus* (Tozer, 1961) at Botneheia, Sassenfiord, and at Kap Thordsen indicates that we are dealing with a late Scythian horizon equivalent to the *Olenekites* fauna of northern Siberia.

The *Olenekites* fauna contains at least three species of *Svalbardiceras*, *S. schmidti* (Mojsisovics), *S. dentosus* (Mojsisovics) and *S. sibiricum* (Mojsisovics). Popov (1961) established the genus *Nordophiceras*—type species *Xenodiscus karpinskii* Mojsisovics (1886, p. 87, pl. 11, fig. 13)—for a variety of species described by Mojsisovics (1886) as *Xenodiscus schmidti*, *Xenodiscus dentosus*, and *Xenodiscus euomphalus*. Thus within the genus *Nordophiceras*, Popov (1961) combined what I consider to be a heterogeneous assemblage of species including forms with rounded venters and others with flat venters. Popov (1961) recognized that *Xenodiscus schmidti* was very similar to *Svalbardiceras spitzbergensis* Frebold, but, on the argument that the suture of this latter species was unsatisfactorily defined, and that the suture was unknown, he felt a comparison was not possible. It is true that no drawing of the suture was presented with the original description of *Lecanites* (?) *spitzbergensis* Frebold (1929b, p. 299, pl. 1, fig. 1), but they are visible on the photograph of the specimen. Frebold interpreted the lobes of this specimen as being goniatitic. One of the two specimens from Kap Thordsen, which Frebold (1929a) described as *Ammonites* sp. indet., I believe is conspecific with the type of *Svalbardiceras*; it has two denticulated lateral lobes and a smooth auxiliary lobe on the umbilical wall. *Nordophiceras* should be restricted to forms with rounded venters like the type species *Xenodiscus karpinskii* Mojsisovics. Both the Spitsbergen and the Olenek species of *Svalbardiceras* are known from very few specimens. *Svalbardiceras schmidti* differs from *S. spitzbergensis* mainly in being more involute.

Of the other two species of *Svalbardiceras* in the Olenek fauna, *S. dentosus* is unique for the low clavi along its sharp ventral shoulders, and *S. sibiricum* for its great involution of the conch. The latter species was first listed by Popov (1961, p. 7) as a representative of *Boreomeekoceras*, and later (Popov, 1962a, p. 176, 186) as a species of *Hemiprionites*. Tozer (1965, p. 37) has correctly pointed out the errors of these identifications.

Recently Tozer (1965) has described *Svalbardiceras freboldi*, from beds with *Olenekites* on Ellesmere Island, and *Svalbardiceras chowadei*, from the Toad Formation of British Columbia, in actual or close association with *Keyserlingites subrobustus*. These two species differ very little from *S. spitzbergensis* and *S. schmidti*.

A fragmentary specimen from the Upper Thaynes Formation has been recorded by Kummel (1954, p. 187) as *Svalbardiceras* sp. The description of this species is in manuscript awaiting publication. The specimen came from a fauna which included species of *Keyserlingites* and *Prohungarites*.

The *Columbites* fauna of southeastern Idaho has yielded a single well preserved specimen of a new species of *Svalbardiceras*. The description of this species is also in manuscript awaiting publication.

The known species of *Svalbardiceras* are confined mainly to the circum-arctic region and to the cordilleran belt of western North America. The specimens from West Pakistan are too fragmentary to identify at a species level or to make significant comparisons with the other species of the genus. It suffices to say that all of the known species of *Svalbardiceras* appear to form a close genetic unit, and that morphological differences between species are not very great. Finally, the stratigraphic position of all species is clearly late Scythian.

Occurrence. From an 8 foot bed of limestone 126 feet above the base of the Narmia Member (bed no. 34) of the Mianwali Formation, Nammal Gorge, West Pakistan.

Repository. Figured specimen (Pl. 2,

figs. 6–9) MCZ 9587; unfigured specimen MCZ 9588.

Genus *Dagnoceras* Arthaber, 1911
Type species, *Dagnoceras nopcsanum* Arthaber, 1911

Dagnoceras cf. *zappanense* Arthaber
Plate 3, figures 9, 10

Dagnoceras zappanense Arthaber, 1911, p. 241, pl. 21(5), figs. 8, 9; Diener, 1915, p. 115; Spath, 1934, p. 268–271, pl. 7, fig. 2, text-fig. 93d, e, f.

This species is recognized on the basis of a fragmentary specimen of one-third volution, preserved only on one side. One suture is clearly visible and the remainder of the specimen is presumably body chamber. The venter is rounded, ventral and umbilical shoulders also rounded, the flanks broadly convex. There is a single broad, low, bulge starting at the umbilical shoulder and extending half way down the flank. The specimen is identified mainly on its very distinctive suture which consists of a long, narrow, first lateral lobe on the mid region of the flanks, and a small second lateral lobe on the umbilical shoulder (Fig. 22A).

In terms of whorl shape and suture, this specimen is most similar to *Dagnoceras zappanense* Arthaber from the *Subcolumbites* fauna of Albania. *Dagnoceras* is represented in the Albanian fauna by two species—*D. zappanense* and *D. nopcsanum* Arthaber. The former species is also known from the *Albanites* fauna of Timor. The genus is also known from Kwangsi, China, in beds associated with *Hellenites, Prenkites*, etc. (Chao, 1959). As yet, very few species and specimens of the genus are known, but all the specimens known to date are from the late Scythian.

Occurrence. From a 10 foot bed of limestone 17 feet above the base of the Narmia Member (bed no. 30), Mianwali Formation, Narmia Nala, Surghar Range, West Pakistan.

Repository. Figured specimen (Pl. 3, figs. 9, 10) MCZ 9605.

Genus *Stacheites* Kittl, 1903
Type species, *Stacheites prionoides* Kittl, 1903

Stacheites sp. indet.
Plate 3, figure 13

This genus is recognized in the collections from an extremely poorly preserved specimen; were it not for the partial preservation of a very distinctive suture, the specimen never could have been identified. The specimen has an approximate diameter of 29 mm; even though it is crushed it appears to have been a compressed form; the venter is not preserved on any part of the specimen. The umbilicus has a diameter of approximately 5 mm. The suture is shown on Figure 22D. The absence of denticulation is clearly a result of the weathered nature and poor preservation of the specimen; at the same time, I believe the basic outline and pattern of the suture is essentially correct.

Stacheites has now been recorded from a number of localities in Upper Scythian strata. There has long been some confusion surrounding this genus, as Kittl's original figure (1903, p. 27, pl. 4, fig. 8) of the type specimen (*S. prionoides*) was a highly reconstructed drawing with no view of the venter nor any statement in the text as to the character of the venter. The type is a compressed specimen but obviously crushed. The opposite side of the conch is completely missing. The venter is narrow, flattened and sulcate, bordered by acute ventral shoulders. *Stacheites prionoides* is part of the *Tirolites* fauna from the Werfen fauna of Muć, Dalmatia.

Among the species of *Stacheites* that I recognized as valid, the type species is morphologically most similar to a species (in manuscript) from the Tobin Formation of Nevada. The American species is quite similar in the shape of the conch, degree of inflation of the whorls, involution, and suture; the shell, however, has sigmoidal ribs on the flank. The fauna from the Tobin Formation contains *Subcolumbites, Ussuri-*

tes, Arnautoceltites, and *Isculitoides,* among others, all genera characteristic of the Upper Scythian.

The *Subcolumbites* fauna of Kwangsi, China, contains one species of *Stacheites*— *S. latilobatum* (Chao, 1959). This is a valid species of the genus.

Astakhova (1960a, b) records *Stacheites prionoides* Kittl from the highest Scythian beds on the Mangyshlak Peninsula. Unfortunately, she did not describe nor illustrate her specimens. The associated species include *Arnautoceltites bajarunasi* (Astakhova) and *Leiophyllites radians* (Astakhova).

The Pakistan specimen recorded here cannot be closely compared in terms of conch form with any of the recognized species of *Stacheites* because of its poor preservation. The suture, however, even though it is weathered, does show a marked similarity in basic plan to that of other species of *Stacheites.*

Occurrence. The single specimen came from a five foot limestone bed 38 feet above the base of the Narmia Member (bed no. 32) of the Mianwali Formation, Narmia Nala, Surghar Range, West Pakistan.

Repository. Figured specimen (Pl. 3, fig. 13) MCZ 9609.

Genus *Nordophiceras* Popov, 1961
Type species, *Ceratites euomphalus* Keyserling, 1845

Nordophiceras planorbis (Waagen), 1895
Plate 4, figures 1–3

Lecanites planorbis Waagen, 1895, p. 278, pl. 39, fig. 3.
Meekoceras (Gyronites) planorbis, -Diener, 1915, p. 197.

This is another of the many species that Waagen (1895) established on a single specimen. His illustration of the specimen is highly idealized and a photograph of the type is shown on Plate 4, figure 1. The specimen is a cast, in sandstone, with one side buried in matrix. The conch is evolute with compressed, somewhat oval whorls. The venter is rounded, and the umbilical shoulder is well rounded. The specimen

measures 54 mm in diameter, 19 mm for the height of the adoral whorl, and 18.8 mm for the width of the umbilicus. The few adoral sutures are clearly exposed and can be seen in the photograph. Waagen concluded that the two lateral lobes were without any denticulation and that there was a straight auxiliary series. The region of the umbilical shoulder is so weathered that all features there are blurred and this accounts for the nature of the suture at that place. As for the rest of the suture the basic shape of the first and second lobes and saddles is probably essentially correct, but the absence of denticulation of the lobes is, on my inspection of the specimen, due clearly to weathering.

In addition to Waagen's type specimen I have three specimens collected from the same horizon and locality as Waagen's type. Unfortunately, none of these specimens are as well preserved as Waagen's type and they expose nothing but highly weathered sutures. The best preserved of these specimens (Pl. 4, figs. 2, 3) is about the same size as the type and is identical with the type specimen in all essential features.

Recognition of the genus *Nordophiceras* has aided greatly in our interpretation of late Scythian faunas. The genus includes a number of species previously included in *Meekoceras, Ophiceras, Prionolobus,* and *Xenodiscus* among others; all are genera thought to be confined to the lower half of the Scythian. Popov (1961, p. 39) included in his new genus *Nordophiceras,* besides the type species, *Xenodiscus karpinskii* (Mojsisovics, 1886), *Xenodiscus schmidti* Mojsisovics, *Xenodiscus dentosus* Mojsisovics, *Xenodiscus euomphalus* Mojsisovics, and *Nordophiceras alexeevae* Popov. Of these species, *X. schmidti* and *X. dentosus* are quite different from the type species, *X. karpinskii,* and are more properly species of *Svalbardiceras* Spath; also *X. karpinskii* cannot be separated from *X. euomphalus* which is an older species name. Thus, of these Siberian species, only two are valid species of *Nor-*

dophiceras, the type—*N. euomphalus*—and *N. alexeevae*. These two species, according to Popov (1961), are confined to his *Dieneroceras* Zone. They differ in that *N. euomphalus* is smooth, and *N. alexeevae* has prosiradiate ribs on the inner whorls. *Nordophiceras euomphalus* is quite similar to *N. planorbis* in its basic conch architecture. There is a remarkable parallelism of these two Siberian species with two species from the *Columbites* fauna of southeastern Idaho, namely *Prionolobus jacksoni* Hyatt and Smith (1905, p. 151, pl. 62, figs. 11–21) and *Meekoceras pilatum* Hyatt and Smith (1905, p. 155, pl. 63, figs. 3–9). *Prionolobus jacksoni* is very similar to *Nordophiceras euomphalus* and perhaps even conspecific. The extremely small sample of *N. euomphalus* prevents conclusive analysis of this relationship. *Meekoceras pilatum*, on the other hand, is an ornamental species of *Nordophiceras* on the same pattern as *N. alexeevae*. The close relationship of these species is part of the reason I believe the north Siberian fauna, that Popov assigns to his *Dieneroceras* Zone, is *Columbites* Zone in age, and not equivalent to the *Anasibirites* Zone as advocated by Popov. These species are older by at least one zone from what I believe to be the age of *N. planorbis*.

There is one other Siberian species that has at least a superficial similarity to *N. planorbis* and this is *Arctoceras simplex* (Mojsisovics) in Popov (1961, p. 67, pl. 17, fig. 1). I fail to find any justification for this identification. The Spitsbergen specimens of *Arctoceras simplex* described by Mojsisovics are inner whorls of *Arctoceras blomstrandi* (Lindström), and of mid-Scythian (*Meekoceras* Zone) age (Kummel, 1961). Popov's specimen is from the *Olenekites* Zone. It appears to be a valid species of *Nordophiceras* and is quite similar in conch form, etc., to *N. planorbis*. Popov (1961, p. 68) states that there are sparse radial ribs disappearing on the body chamber on his species; this feature is not apparent, however, on the illustration of the species.

Occurrence. Waagen's type specimen and the three specimens recorded here came from sandstone beds of the Narmia Member above the hard "Bivalve limestone" on the east side of Chhidru Nala, Salt Range, West Pakistan.

Repository. Holotype (Pl. 4, fig. 1) GSI 7226; topotype (Pl. 4, figs. 2, 3) MCZ 9611; unfigured topotypes MCZ 9612.

Nordophiceras cf. planorbis (Waagen), 1895
Plate 4, figures 4, 5

Two specimens were collected from the Narmia Member in the Surghar Range which are possibly conspecific with the specimens of *Nordophiceras planorbis* from this member at Chhidru in the Salt Range. However, the poor preservation of these specimens and differences in morphological appearance suggest separate treatment for the time being at least. The main apparent differences are a slightly greater degree of evolution of the conch, more compressed whorls, and less distinct umbilical shoulders. The suture is shown on Figure 22B. All of these features, though, are affected to a greater or lesser degree by the state of preservation.

Occurrence. The specimen illustrated on Plate 4, figure 4, came from a 10 foot bed of limestone, 17 feet above the base of the Narmia Member (bed no. 30) in Narmia Nala, and the specimen shown on Plate 4, figure 5, came from a 7 foot bed of limestone 40 feet above the base of the Narmia Member (bed no. 9), Landa Nala, Surghar Range, West Pakistan.

Repository. MCZ 9613 (Pl. 4, fig. 4), MCZ 9614 (Pl. 4, fig. 5).

Genus Arctomeekoceras Popov, 1962
Type species, Meekoceras rotundatum Mojsisovics, 1886

Arctomeekoceras sp. indet.
Plate 2, figures 1–5

This species is represented by the largest number of specimens collected from the

Narmia Member of the Mianwali Formation. The preservation in most cases is much poorer than that of the other species in the fauna. Morphologically, this species is not very distinctive making identification difficult and perhaps even tenuous. The conch is compressed and involute. The venter is narrowly rounded on the younger whorls and appears to become more broadly rounded during growth, reflecting a slight inflation of the whorls. The ventral shoulders in either stage are rounded. The umbilical shoulder, however, is abruptly rounded and the umbilical wall is vertical. No surface markings, as growth lines, etc., are present on any of the specimens. The suture is shown on Figure 22E.

There are no species in the late Scythian faunas of Tethys, as for instance of Albania, Chios, or Timor, that bear any resemblance to this Pakistan species. It is within the *Olenekites* fauna of northern Siberia where one can recognize morphologically similar forms. Mojsisovics (1886) first described from the Olenek fauna a number of species which he placed in the genera *Meekoceras* and *Xenodiscus*. These are an interesting assemblage of species that most Triassic students have had difficulty in interpreting. Very few comparable species types have turned up in other late Scythian deposits. Spath (1934) suggested that several of these species probably represented new and distinct generic groups but refrained from any further action. It is through the publications of Yu. N. Popov (1961, 1962a) that we have much new data on the Olenek fauna. From among the original group of species which Mojsisovics assigned to *Meekoceras* and *Xenodiscus*, Popov has introduced three new generic names. These are: *Boreomeekoceras* Popov (1961, p. 41)—type species *Meekoceras keyserlingi* Mojsisovics (1886, p. 81, pl. 10, fig. 11), *Nordophiceras* Popov (1961, p. 38)—type species *Xenodiscus karpinskii* Mojsisovics (1886, p. 75, pl. 11, fig. 13), and *Arctomeekoceras* Popov (1962a, p. 186, pl. 1, figs. 1, 5)—type spe-

cies *Meekoceras rotundatum* Mojsisovics (1886, p. 83, pl. 10, fig. 16). Within his genus *Nordophiceras*, Popov included a heterogenous group of species; those species allied to the type species with rounded venters are confined to Popov's *Dieneroceras* Zone. The flat ventered species (e.g. *X. schmidti*) are confined to the *Olenekites* Zone and should be placed in *Svalbardiceras*. *Boreomeekoceras* is characterized by forms with involute compressed conchs, narrowly rounded venter, and a suture with a long serrated auxiliary series. *Arctomeekoceras* is likewise an involute, compressed form but the venter is broader, the umbilical shoulder more sharply rounded, and the suture with a short auxiliary series. In the Siberian region *Arctomeekoceras* is known only from the *Olenekites* Zone.

All of these arctic species are as yet known by relatively few specimens and there is no question but much more data is needed. The Pakistan specimens recorded here are more similar to *Arctomeekoceras rotundatum* than to any other species of late Scythian ammonoid. The incompleteness of the sample and general poor preservation prevent a more detailed analysis.

Occurrence. This species has been collected from three localities in the Narmia Member of the Mianwali Formation: (1) from a 3.5 foot bed of limestone 20 feet above the base of the Narmia Member (bed no. 5) in Landa Nala, Surghar Range; (2) from a 10 foot bed of limestone 18 feet above the base of the Narmia Member (bed no. 30) in Narmia Nala, Surghar Range; and (3) from an 8 foot bed of limestone 126 feet above the base of the Narmia Member (bed no. 34) in Nammal Gorge, Salt Range, West Pakistan.

Repository. Figured specimens (Pl. 2, figs. 1, 2) MCZ 9584, (Pl. 2, figs. 3, 4) MCZ 9585, (Pl. 2, fig. 5) MCZ 9586; unfigured specimens from Landa Nala MCZ 9590, 9592, from Narmia Nala MCZ 9589, from Nammal Gorge MCZ 9591.

Family TIROLITIDAE Mojsisovics, 1882
Genus *Tirolites* Mojsisovics, 1879
Type species, *Tirolites idrianus* Hauer, 1865

Tirolites sp. indet.
Plate 4, figures 8, 9

The collections contain a single specimen that in spite of its poor preservation can be assigned to the genus *Tirolites*. The conch is evolute with subrectangular whorl sections. The venter is broad, very low arched. Along the ventral shoulder are nodes that clearly are extensions of ribs. Unfortunately, the whorl sides from the mid section to the umbilical seam are not at all well preserved, but there is faint indication that these ribs extend across much of the flank. Of the suture only the first lateral saddle is visible, and this lies across the ventral shoulder.

Tirolites is the principal genus of the Alpine Werfen fauna. It has been traditional to place the *Tirolites* fauna between the *Owenites* Zone and the *Columbites* Zone in our Scythian chronological scheme. The genus, however, has been recorded from several upper Scythian faunas. For instance, it is present in the *Columbites* fauna of southeastern Idaho (Smith, 1932), the *Ussurites* fauna in the Confusion Range, Utah (Silberling, *in* Hose and Repenning, 1959, p. 2189), and the *Subcolumbites* fauna of Albania (Arthaber, 1911). The biology and stratigraphic range and significance of the genus is in need of a thorough revision.

Occurrence. From micaceous sandstone bed 17 feet above base of Narmia Member (bed no. 29) of Mianwali Formation, Nammal Gorge, Salt Range, West Pakistan.

Repository. Figured specimen (Pl. 4, figs. 8, 9) MCZ 9615.

Family HUNGARITIDAE Waagen, 1895
Genus *Prohungarites* Spath, 1934
Type species, *Prohungarites similis* Spath, 1934

Prohungarites cf. *crasseplicatus* (Welter), 1922
Plate 3, figures 11, 12

Hungarites crasseplicatus Welter, 1922, p. 147, pl. 168(14), figs. 1–6.
Prohungarites crasseplicatus, -Spath, 1934, p. 244; Spath, 1951, p. 20; Kummel, 1961, p. 525.
Hungarites cf. *middlemissii* Diener, *in* Welter, 1922, p. 146, pl. 13, figs. 6–9, 18.
Prohungarites similis Spath, 1934, p. 327; Spath, 1951, p. 19; Kummel, *in* Arkell et al., 1957, p. L155, fig. 187, 6.

Four small phragmocones of fair preservation from the Narmia Member exposed at its type locality in Narmia Nala are in the collections. The better preserved of the four specimens (Pl. 3, figs. 11, 12) measures approximately 30.5 mm in diameter, 11.3 mm for the width of the adoral whorl, 12.8 mm for the height of the whorl, and 8.5 mm for the diameter of the umbilicus. The conch is fairly evolute with compressed whorls. The whorl flanks are flattened and converge slightly toward the venter. The venter is low and broadly rounded as are the ventral shoulders. The umbilical shoulders are more sharply rounded and the umbilical wall is vertical. The whorl flanks bear low, broad radial ribs that extend from the umbilical to the ventral shoulders. On the inner volutions, at a diameter of 8 mm, the venter is acute and the whorl sides broadly convex. The suture (Fig. 22C) consists of a broad, prominent first lateral lobe, a much smaller second lateral lobe and a very small auxiliary lobe on and just above the umbilical shoulder.

Spath (1934, p. 327) introduced the generic name *Prohungarites* for *P. similis* Spath (= *Hungarites* cf. *middlemissii* Welter (non Diener) 1922). This species along with *Hungarites crasseplicatus* Welter (1922) comprise an interesting keeled group of ammonoids from the blocks with the manganese coated fossils at Nifoekoko, Timor. These two species were originally separated merely on differences in the intensity of the ribbing. Even Welter (1922, p. 147) discussed the gradational aspects of these species and illustrated one specimen (Welter, 1922, pl. 167 (13), figs. 10, 11) as a transitional form between *Hungarites* cf. *middle-*

missii and *Hungarites crasseplicatus*. Re-study of Welter types shows that his descriptions and illustrations of these species are quite adequate. There appears no doubt but that these two species are synonymous. I would also place in the synonymy of *P. crasseplicatus* the specimen Kiparisova (1961, p. 160, pl. 31, fig. 5) described as *Prohungarites* (?) *popovi* from an horizon she characterized as the end of the Olenek stage (Upper Scythian) or the beginning of the Anisian.

The Pakistan specimen recorded here differs from the Timor *P. crasseplicatus* principally in the absence of any indication of a keel along the central part of the venter on the mature whorls. In all other conch features, such as shape of the whorl section, shape of the ventral and umbilical shoulders, and nature of the umbilical wall, it is very similar. The suture is likewise essentially the same. The other Timor species of *Prohungarites, P. tuberculatus* (Welter), is more robust with a more highly developed ornamental pattern.

There is a stronger morphological similarity to a species from the upper Thaynes Formation of southeastern Idaho that I have previously recorded as *Prohungarites* n. sp. cf. *P. crasseplicatus* Welter (Kummel, 1954, p. 187). This species will be fully documented in another publication. It is very similar to the Pakistan species in most essential features. Whereas I believe the Pakistan and Idaho forms are distinct species, at the same time they are extremely closely related. Both species have acute venters only on the earliest volutions and rounded venters on the later volutions. It is mainly in this feature that these two species are distinct from *P. crasseplicatus* from Timor.

Occurrence. The four specimens came from a 10 foot limestone bed, 17 feet above the base of the Narmia Member (bed no. 30) of the Mianwali Formation in Narmia Nala, Surghar Range, West Pakistan.

Repository. Figured specimen (Pl. 3, figs. 11, 12) MCZ 9606, unfigured specimen MCZ 9607.

APPENDIX

Stratigraphic section of Triassic Formation exposed on north side of small creek 200 yards east of road, one-quarter mile southeast of Kathwai, Salt Range, West Pakistan (Figs. 6, 7).

Bed No.	Thickness Feet

MIANWALI FORMATION (Lower Triassic)

Mittiwali Member

7.	Shale, olive-gray, mostly covered	30.0
6.	Limestone, gray, fine-grained, co-quinoidal, thin-bedded, slightly glauconitic, poorly preserved ammonites (*Gyronites*, etc.)	5.9
	Total 35.9	

Kathwai Member

|		
5.	Limestone, tan and gray, fine-grained, faintly glauconitic; contains brachiopods and echinoderm fragments	1.0
4.	Limestone, yellow-brown, thin-bedded, soft, coquinoidal, contains ammonites (*Ophiceras*), *Orbiculoidea*, rhynchonellid brachiopods, echinoid spines, crinoid fragments; most fossils come from six inch bed one foot from top of unit	5.0
3.	Limestone, yellow-brown, highly dolomitic, echinodermal, massive, weathers rust brown	1.0
2.	Dolomite, like unit 1 but in beds one to two inches thick	2.9
1.	Dolomite, yellow-brown, massive, fine-grained, weathers rust brown,	

Figure 6. Locality map of Kathwai region, Salt Range, West Pakistan showing distribution of late Permian and Triassic formations. Geologic data from unpublished map by E. R. Gee.

Figure 7. Unnamed nala two miles south of Kathwai, Salt Range, West Pakistan. The bench in the mid-part of the photograph is formed by the Kathwai Member and the "Lower Ceratite limestone" of the Mianwali Formation.

contains *Glyptophiceras, Orbicu-loidea*, large smooth pectins; fossils come from upper six inches of unit   2.6
<div align="right">Total 12.5</div>
<div align="right">Total Mianwali Formation 48.4</div>

CHHIDRU FORMATION (Upper
   Permian)
  00. Sandstone, white, soft, weathers
     yellow
  0. Limestone, gray, sandy, massive,
     with abundant Permian fossils; on
     west side of nala, fifty yards off

this unit immediately underlies unit 1 and the white friable sandstone   2.6
is absent

Stratigraphic section of Triassic formations exposed 1.5 miles southeast of Kufri, 0.5 miles north of highway marker 31 on road from Kuraddi to Kathwai (Figs. 8, 9).

Bed No.   Thickness
                                           Feet

2.6-0   MIANWALI FORMATION (Lower
         Triassic)
         Narmia Member
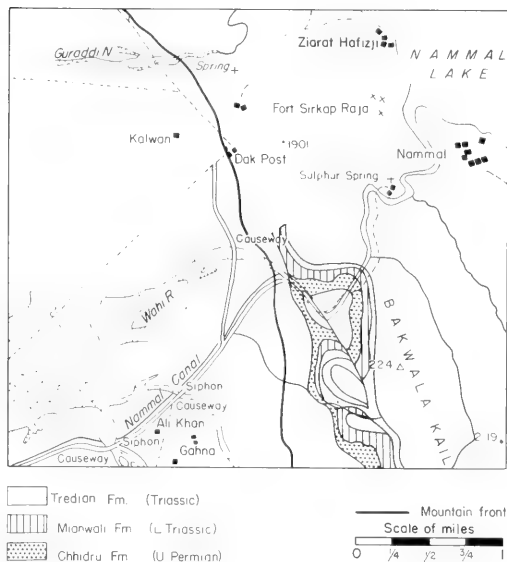   12. Limestone, light gray, fine-grained,
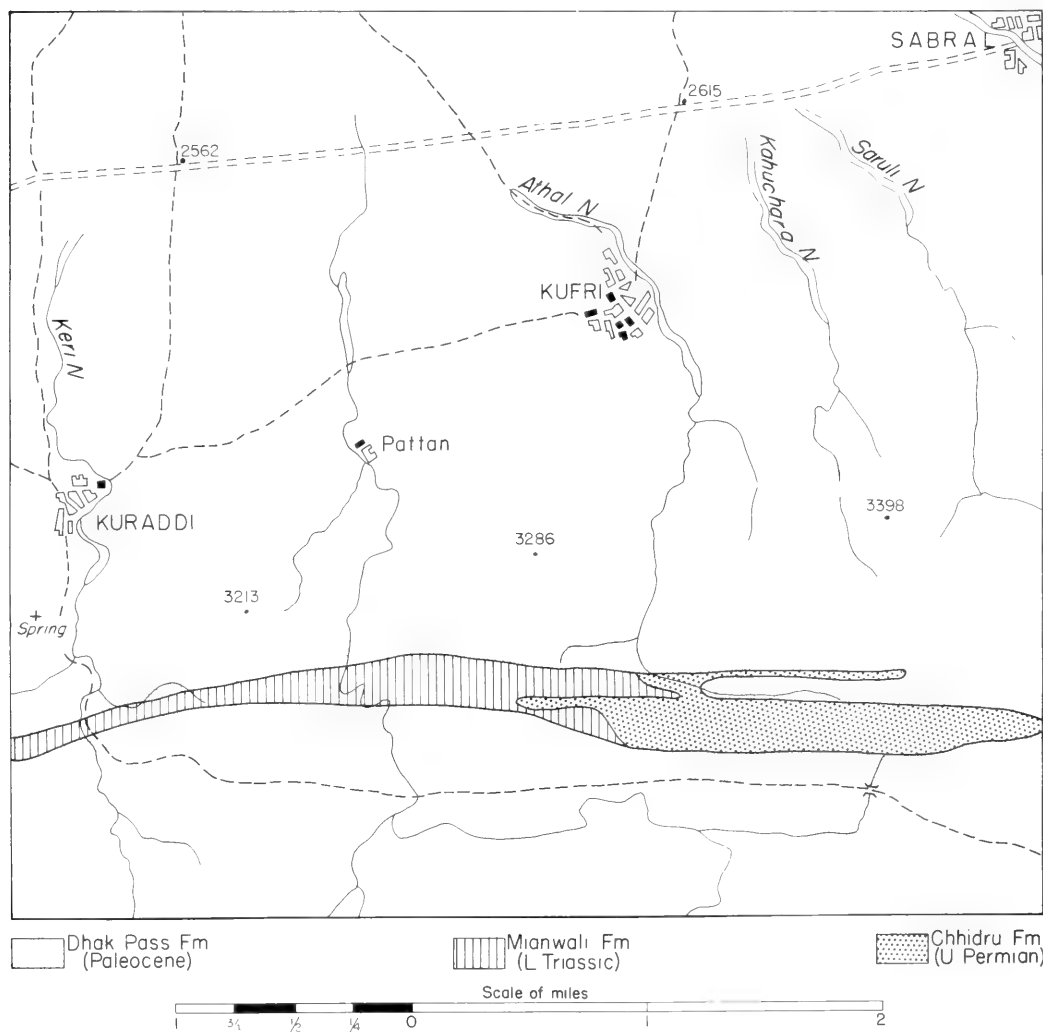
Figure 8. Locality map of Kufri region, Salt Range, West Pakistan, showing distribution of late Permian and Triassic formations. Geologic data from unpublished map by E. R. Gee.

Figure 9. The Kufri locality in the Salt Range of West Pakistan. The hills in the right half of the photograph are made up of the Chhidru Formation; the dip slope of these hills is held up by the Kathwai Member and the "Lower Ceratite limestone"; the saddle is underlain by the "Ceratite marls" and the following slope the "Ceratite sandstone" and the "Upper Ceratite limestone"; the face of this ridge is formed by the "Bivalve limestone" of the Narmia Member and this is overlain by the Dhak Pass Formation of Paleocene age.

very hard, massive, a coquina of pelecypods. This is the Bivalve limestone of Waagen; here overlain by Eocene limestones   10.0
                                        Total 10.0

Mittiwali Member

11. Sandstone, iron-brown, massive, hard, has traces of poorly preserved pelecypods   4.0
10. Covered, probably shale   6.0
 9. Limestone like bed 8, in beds one foot thick, separated by shale interbeds; contains ammonites (*Stephanites* and *Anasibirites*)   25.0
 8. Limestone, gray, fine-grained, sandy, hard, in beds 4–6 inches thick, separated by one inch beds of tan, silty shale, also a few beds of tan fine-grained sandstone; contains many poorly preserved ammonites   30.0
 7. Covered, interval includes much of the Ceratite marls and the Ceratite sandstone   115.0
 6. Shale, olive-gray, with 4–6 inch beds of hard, argillaceous, olive limestone, fossiliferous   20.0
 5. Limestone, gray, thin-bedded; con-

tains numerous poorly preserved ammonites   4.0
                                        Total 204.0

Kathwai Member

 4. Limestone, gray, thin-bedded, with an occasional poorly preserved ammonite (*Ophiceras?*) and *Orbiculoidea*   1.5
 3. Dolomite, gray-brown, massive, hard, weathers brown; contains cidarid spines and small brachiopods   1.0
 2. Dolomite as unit 1 but thinner bedded; contains rhynchonellid brachiopods, fish teeth, crinoid fragments, and fucoids   3.0
 1. Dolomite, yellow-brown, sandy, weathers brown; contains poorly preserved pelecypods   10.0
                                        Total 15.5
      Total Mianwali Formation 229.5

CHHIDRU FORMATION (Upper Permian)

00. Sandstone, white, friable, massive, with crinoid remains and shell fragments   2.0
 0. Limestone, gray, sandy, massive, with *Bellerophon*   2.0

Stratigraphic section of basal part of the Triassic Mianwali Formation exposed in Munta Nala, west of Wargal, Salt Range, West Pakistan (Figs. 10–13).

Bed No.	Thickness (in feet)

MIANWALI FORMATION (Lower Triassic)

Mittiwali Member (lower part)

16. Limestone, gray, fine- to medium-grained; very fossiliferous, with small pectinid pelecypods, ammonoids (*Gyronites*, etc.) and fish remains ... 1.0

15. Shale, gray ... 0.8

14. Limestone, yellow-gray, thin-bedded; with numerous ammonoids (*Gyronites*, etc.) ... 1.9

13. Limestone, light-gray, dense, hard, glauconitic, weathers brown ... 0.2

12. Limestone, very light gray, irregular texture, contains large pelecypods, fragments of ammonites, fish teeth ... 1.4

Kathwai Member

11. Sandstone, gray, massive, with a few one-inch calcareous beds ... 3.0

10. Limestone, pinkish-gray, fine-grained; unit begins with four inches of grayish-black shale, followed by three inches of lenticular limestone, then one foot of laminated to thin-bedded sandstone, then limestone; contains small pectinids, ammonoids (*Ophiceras?*), and fish teeth ... 2.5

9. Dolomite, light gray, massive, weathers iron-brown; contains shell fragments, rhynchonellid brachiopods, eumorphotid pelecypods, ammonites (*Ophiceras?*), cidarid spines, fish teeth ... 2.4

8. Shale, dark gray, with laminae of fine, tan sandstone, contains poorly preserved brachiopods, *Campylites?*, and pelecypods ... 1.5
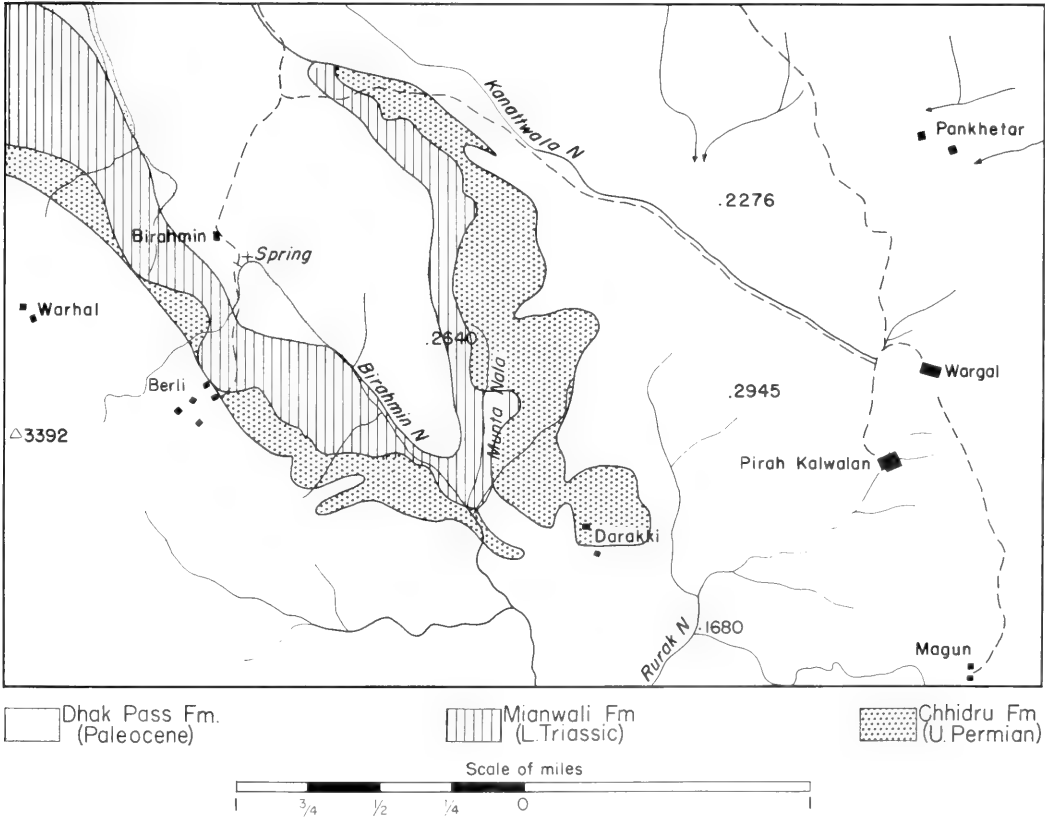
Figure 10. Locality map of Munta Nala (Wargal region), Salt Range, West Pakistan showing distribution of later Permian and Triassic formations. Geologic data from unpublished map by E. R. Gee.

Figure 11. Permian and Triassic formations exposed along Munta Nala, Wargal region, West Pakistan. The dip slope to the right of the nala is formed by the Chhidru Formation; the strata to the left of the nala are the Mianwali Formation.

7. Dolomite, tan, fine-grained, massive, upper one foot laminated, weathers brown   6.0

Total 15.4

CHHIDRU FORMATION (Upper Permian)

6. Shale, dark gray, micaceous, with thin beds of cross-bedded sandstone and laminae of sandstone   5.9

5. Sandstone, white, massive, friable, lenticular, bed ranges in thickness from two inches to one foot   1.0

4. Shale, dark gray, clay, with laminae of fine sandstone and thin beds of micaceous sandstone; contains plant fragments   3.0

3. Sandstone, yellowish gray, calcareous, massive, weathers tan, unit lenticular ranging in thickness from four inches to three feet, contains *Bellerophon* and other typical Permian fossils   3.0

2. Shale, dark gray, clay, micaceous, with laminae of fine-grained, very pale orange sandstone and one inch to one foot beds of cross-bedded

sandstone; contains spectacular slump structures and plant fragments   6.0

1. Sandstone, very light gray, massive, calcareous, with numerous pockets of typical Permian fossils and worm borings   4.0

Stratigraphic section of Triassic formations exposed on the west side of Chhidru Nala, Salt Range, West Pakistan (Figs. 14, 15).

Bed No.	Thickness Feet

MURREE FORMATION (Miocene)
Sandstone, variegated
MIANWALI FORMATION (Lower Triassic)
Narmia Member

26. Dolomite, red and yellow-brown, medium grained, massive, unit hard and a ridge former   10.0

25. Sandstone, pink and violet toward base, remainder white, calcareous, fine-grained, massive, soft, friable, a few two foot beds of shale   37.0

24. Shale, gray and olive, with siltstone, unit poorly exposed   23.0
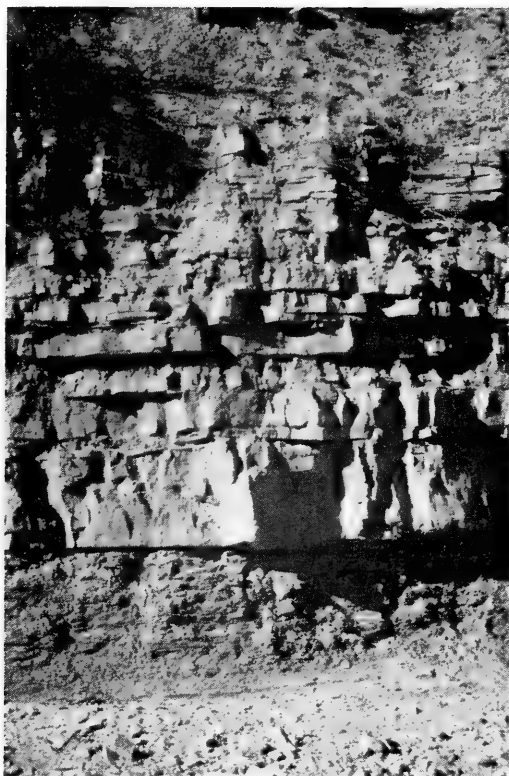
Figure 12. The Permo-Triassic contact beds along Munta Nala near Wargal, Salt Range, West Pakistan. The shaly beds at the bottom of the ledge are part of the white sandstone unit of the Chhidru Formation and the overlying massive strata are the dolomite beds of the Kathwai Member.

Figure 13. Mianwali Formation exposed in Munta Nala. Uppermost hard layer is Dhak Pass Formation of Paleocene age.

23. Sandstone, tan to rust-brown, some thin red units, calcareous, thin evenly bedded, micaceous, unit soft, not well exposed, probably includes beds of sandy shale or shaly sandstone; contains ammonites (*Xenoceltites sinuatus, Nordophiceras planorbis*) and orthocerids   40.0

22. Limestone, light gray, very hard, massive, weathers rusty-gray, a coquina of pelecypods for the most part, also contains poorly preserved ammonites, upper six inches of unit contains numerous nautiloids including *Enoploceras* and orthocerids   5.0

21. Sandstone, yellow-brown, a coquina of pelecypods; this unit plus unit 22 make up the Bivalve bed of Waagen   3.5
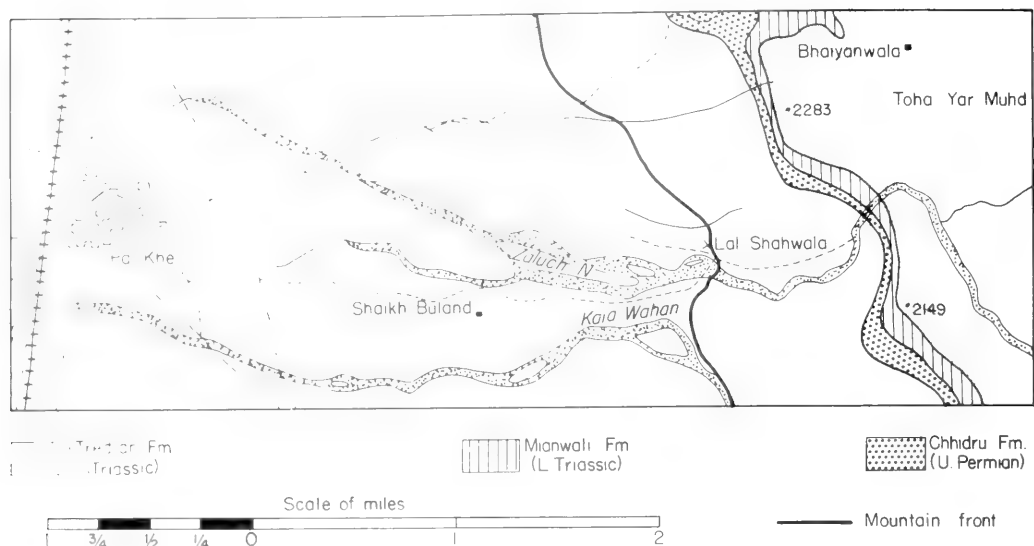
Total 118.5
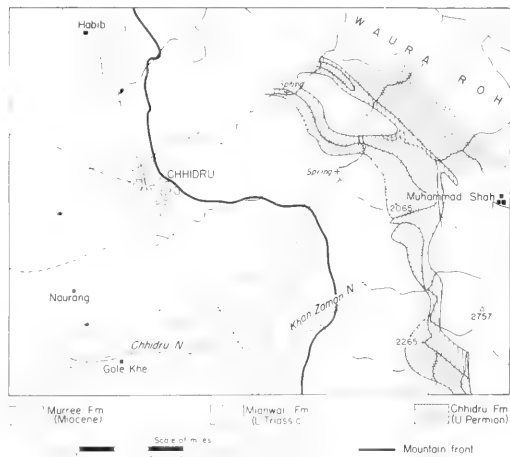
Figure 14. Locality map of Chhidru Nala, Salt Range, West Pakistan, showing distribution of late Permian and Triassic formations. Geologic data from unpublished map by E. R. Gee.

Figure 15. Triassic Formation on east side of Chhidru Nala, Salt Range, West Pakistan. The hard units forming the crest of the ridge are the "Upper Ceratite limestone." The uppermost of these hard beds is the "Bivalve limestone" and the following slope is made up of shale and sandstone beds of the Narmia Member.

Mittiwali Member

20. Sandstone like bed 19, but very thinly bedded, no fossils seen   2.5

19. Sandstone, yellow-brown, fine-grained, massive; contains poorly preserved ammonites   2.5

18. Sandstone, gray and tan, fine-grained, in thin beds, with numerous beds of gray limestone which contain ammonites   33.0

17. Limestone, gray, thin- to medium-bedded, some beds of sandstone, unit very fossiliferous, but preservation poor   47.0

16. Sandstone, gray, tan, massive to thin-bedded, mostly covered   45.0

15. Shale, black to olive, with numerous thin beds of micaceous sandstone and argillaceous limestone, fossiliferous   125.0

14. Limestone, gray, hard, very fossiliferous, *Gyronites*, etc.   1.6

13. Shale, black, with thin beds of fine-grained, tan sandstone, mostly covered   3.0

12. Limestone, gray, fine-grained, hard, thin- to medium-bedded, very fossiliferous, *Gyronites*, etc., but preservation poor   3.0

Total 262.6

Kathwai Member

11. Sandstone, tan, fine-grained, laminated   0.2

10. Limestone, gray, coquinoidal, consisting of pelecypods, brachiopods, and gastropod fragments; contains fairly well preserved ammonites and pelecypods   0.9

9. Limestone, grayish-tan, fine-grained, thin-bedded, scoured in part, dolomitic, with minor amounts of glauconite   2.0

8. Sandstone, grayish-tan, fine-grained, thin-bedded, with 2 inch bed of limestone in center containing *Ophiceras connectens*   2.5

7. Limestone, light gray, hard, fragmental; contains rhynchonellids and ammonites (*Ophiceras*)   1.0

6. Shale, olive-gray, with some thin sandstone beds   1.0

5. Limestone, gray, hard, contains brachiopods, crinoid remains, ciderid spines, teeth and bone fragments   1.0
4. Dolomite like bed 3, but harder; contains fossil fragments   1.3
3. Dolomite, tan, fine-grained, thin-bedded, shaly, unit soft   0.8
2. Dolomite, tan, medium to massively bedded, sandy in lower part; contains fossil fragments   2.5
1. Dolomite, tan, mottled, sandy, hard, massive   3.6

Total 16.8
Total Mianwali Formation 397.9

CHHIDRU FORMATION (Upper Permian)

00. Sandstone, white, fine-grained, friable, with echinoderm fragments and poorly preserved pelecypods   12.0
0. Limestone, gray, sandy, with abundant bellerophons, productids, and other typical Permian forms

Stratigraphic section of Triassic formations exposed in Nammal Gorge, Salt Range, West Pakistan (Figs. 16, 17, 18).

Bed No.   Thickness Feet

TREDIAN FORMATION (?Lower and ?Middle Triassic)

Khatkiara Member
44. Sandstone, white, massive
Landa Member
43. Sandstone, tan to red, thin-bedded to massive, parts laminated, contains ripple marks and abundant slump structures   28.0
42. Sandstone, tan, red in part, massive, cross-bedded, alternating with sandy, micaceous shale containing plant fragments   8.0
41. Shale like bed 39 but with fewer and thinner hard beds   27.0

Total 63.0

MIANWALI FORMATION (Lower Triassic)

Narmia Member
40. Dolomite, gray, sandy in part, massive, weathers rust-brown, one incomplete and poorly preserved ammonite collected   5.0
39. Shale, gray and black, with several one-foot beds of gray, sandy limestone that weather rust-brown   22.0
38. Sandstone, pink, massive, in part laminated, weathers rust-brown, no fossils seen   4.0

Figure 16. Locality map of Nammal Gorge, Salt Range, West Pakistan showing distribution of late Permian and Triassic formations. Geologic data from unpublished map by E. R. Gee.

37. Shale like bed 35   6.0
36. Limestone like bed 34; contains orthocerids, abundant crinoid fragments and worm tracks   6.0
35. Shale, gray-black, silty, with thin beds of laminated calcareous sandstone and 2–6 inch beds of gray limestone; top of unit is one-foot bed of massive sandstone with slump structures; unit contains poorly preserved ammonites and pelecypods   12.5
34. Limestone, gray, very hard, sandy in part, irregularly bedded in part, glauconitic in part; contains poorly preserved ammonites (*Pseudosageceras multilobatum*, *Arctomeekoceras* sp. indet., *Svalbardiceras* sp. indet.), pelecypods, and brachiopods   8.0
33. Shale and sandstone like bed 31, sandstone in part pink   30.0
32. Sandstone, tan, massive, cross-bedded in part, a few thin beds of sandy limestone containing abundant small, poorly preserved pelecypods, a few 6 inch shale beds present   7.5
31. Shale, gray-black, in beds 1–2 feet thick, alternating with tan sandstone showing slump structures   22.0

Figure 17. Mianwali Formation in Nammal Gorge, Salt Range, West Pakistan. The white strata in the lower left-hand corner of the photograph are the upper beds of the Chhidru Formation, the overlying massive beds are the Kathwai Member and the "Lower Ceratite limestone"; then come the "Ceratite marls"; the next massive beds are the "Ceratite sandstone," and the uppermost strata are part of the "Upper Ceratite limestone."

30. Sandstone, tan, fine- to medium-grained, massive 6.5
29. Shale, gray-black, with a few beds of tan, slightly pink, micaceous sandstone and sandy gray limestone, pelecypods and ammonites (*Tirolites* sp. indet.) present but poorly preserved 53.0
28. Limestone, dark to light gray, massive, very hard, coquinoid beds of pelecypods alternate with irregularly bedded limestones that contain brachiopods, ammonites, pelecypods, and gastropods. This unit is intermediate in its lithology between the typical Bivalve bed as seen in Chhidru and the basal limestone beds at Narmia. 7.0

Total 189.5

Mittiwali Member

27. Sandstone, tan, calcareous, fine-grained, thin-bedded, with thin beds of black shale and gray limestone 2.5
26. Limestone, gray, massive, very hard ... 2.0
25. Limestone, dark gray, in beds 1–4 inches thick alternating with 1–4 inch beds of black, micaceous shale and siltstone; contains ammonites (*Anasibirites*) 23.0
24. Limestone, gray, fine-grained, in beds 1–3 inches thick; contains numerous poorly preserved ammonites 16.0
23. Sandstone, tan, fine-grained, thin-bedded, with a few thin interbeds of shale and gray limestone 3.0
22. Limestone, gray, fine-grained; contains poorly preserved ammonites ... 4.0
21. Sandstone like bed 20 but amount of shale greater, individual beds thinner, a few beds of gray limestone 10.0
20. Sandstone, gray, micaceous, fine-grained, some beds grade into gray limestone along strike, numerous interbeds of gray shale 8.6
19. Shale, black and gray, silty, micaceous, with numerous 1–2 inch beds of fine-grained sandstone 4.5
18. Sandstone, tan and gray, fine-grained, with numerous thin, silty shale interbeds; contains poorly preserved ammonites 4.6
17. Siltstone, tan, massive, with some gray limestone 4.0
16. Shale, black, micaceous, with thin laminae of black siltstone and lenticular beds of fine-grained sandstone 3.2
15. Siltstone, gray-black, micaceous, thin-bedded, laminated 3.0
14. Sandstone, tan and gray, calcareous, hard, massive, laminated, with ripple marks 2.3
13. Shale, as bed 11 but with one 2 inch lenticular bed of gray limestone 3.5
12. Sandstone, light tan, massive, cross-bedded 2.2
11. Shale, black, micaceous, alternating with 1–3 inch beds of micaceous, laminated, fine-grained sandstone 9.0
10. Sandstone like bed 9 in beds approximately one foot thick alternating with beds of laminated shaly sandstone 4.0
9. Sandstone, tan and gray, fine-grained, massive 4.0
8. Shale, black, silty, micaceous, with

Figure 18. The Landa Member (lower part of photograph) and Khatkiara Member of the Tredian Formation exposed in Nammal Gorge, Salt Range, West Pakistan.

thin laminae of siltstone and 6 inch beds of fine-grained, lenticular beds of sandstone   8.5

7. Sandstone, light gray, micaceous, fine-grained, cross-bedded, with some thin shale interbeds   3.0

6. Shale, olive-gray to black, micaceous in part, silty in part, with numerous 1–15 inch beds of hard, lenticular argillaceous and sandy limestone; contains few ammonites and pelecypods   118.0

5. Limestone, gray, fine-grained, in beds 1–3 inches thick; contains abundant poorly preserved ammonites   4.0

Total 246.9

Kathwai Member

4. Sandstone, white, thin-bedded, alternating with thin 1–2 inch beds of gray, sandy limestone; contains poorly preserved ammonites (*Ophiceras*) and rhynchonellid brachiopods   2.0

3. Dolomite, gray, sandy, weathers brown, in beds 1–3 inches thick, lower two-thirds of unit contains

cidarid spines and crinoid remains, upper part contains small brachiopods   3.0

2. Dolomite as bed 1, contains cidarid spines and crinoid remains   1.4

1. Dolomite, gray, sandy, massive, weathers brown, no fossils seen   4.6

Total 11.0

Total Mianwali Formation 447.4

CHHIDRU FORMATION (Upper Permian)

00. Shale, black, micaceous, with laminae of tan micaceous siltstone   1.5

0. Sandstone, white, massive, friable   2.0

Stratigraphic section of Triassic formations exposed in Zaluch Nala, Salt Range, West Pakistan (Fig. 19).

Bed No.   Thickness
                                             Feet

TREDIAN FORMATION (?Lower and ?Middle Triassic)

Khatkiara Member

33. Sandstone, white, massive, cross-bedded

Landa Member

Figure 19. Locality map of Zaluch Nala, Salt Range, West Pakistan, showing distribution of late Permian and Triassic formations. Geologic data from unpublished map by E. R. Gee.

32. Sandstone, a mixture of the types that make up beds 27, 28, and 31, in addition purple and red beds, splendid slump structures in upper part, a few beds of dark gray, brown, silty shale   20.0
31. Sandstone, white, massive, with 6 inch rust-brown nodules   2.6
30. Sandstone, like bed 28, reddish in part   6.0
29. Sandstone like bed 27, massive   1.6
28. Sandstone, gray-brown, micaceous, massive, laminated   1.3
27. Sandstone, light gray, massive, laminated, medium-grained, weathers reddish brown   1.0
26. Shale, dark grayish black, silty, with numerous beds of red-brown, laminated, micaceous sandstone, 1–12 inches thick   30.0
                                  Total 62.5

MIANWALI FORMATION (Lower Triassic)
Narmia Member
25. Dolomite, rust-brown, partly gray, weathers rust-brown   2.5
24. Dolomite, gray, very sandy, massive, weathers rust-brown   2.9
23. Shale, black, with thin beds of laminated, micaceous sandstone   7.0
22. Dolomite, gray, sandy, micaceous, massive, laminated, weathers rust-brown   5.0

21. Covered, probably shale   15.0
20. Shale, gray to black, silty, micaceous, with thin beds of hard, dark gray limestone near base; above this are three beds of reddish brown and gray dolomite 1.5, 1.5, and 4 feet thick respectively; one of these beds yielded an orthocerid cephalopod and two poorly preserved ammonites   33.0
19. Limestone, gray, fine-grained, very glauconitic in part, very hard, part of unit a coquina of small pelecypods; lithologic character of unit is a combination of that of the Bivalve beds as seen at Chhidru and the basal limestone at Narmia   10.0
                                  Total 76.4
Mittiwali Member
18. Sandstone, gray, speckled brown, massive   5.0
17. Sandstone, light to dark gray, massive, finely laminated, micaceous and silty, olive, micaceous shale; 12 feet from top of unit there is an 8 inch bed of very hard, dark gray limestone, mottled rust-brown which yielded one ammonite, one nautiloid, and one rhynchonellid brachiopod   55.0
16. Shale, gray and black, with thin beds of gray limestone, weathering brown, unit poorly exposed, some

structural disturbance evident; toward middle of unit are two beds of gray sandy limestone and gray calcareous sandstone, pelecypods present, one ammonite found in float 110.0

15. Limestone, light gray, very hard, in beds 1–6 inches thick, weathers gray, with a few thin laminated beds of gray-black siltstone, numerous poorly preserved ammonites 29.0

14. Sandstone and shale in combination as seen in beds 10, 11, and 12, in units of approximately equal thickness; first have mainly light sandstones, then mainly shales, then mainly sandstones, finally mainly shales, a few thin beds of hard, dark gray limestone, two ammonites collected 31.0

13. Shale, dark olive-gray, silty, micaceous, with a few thin beds of fine-grained sandstone 6.5

12. Sandstone, light gray, micaceous, laminated, with a few beds of gray-black shale 6.0

11. Sandstone like unit 10 but in thinner beds alternating with gray-black, micaceous, shaly siltstone and shale 13.0

10. Sandstone, light gray, fine-grained, massive, laminated, appears to be calcareous, with several 4 inch beds of olive, micaceous siltstone 9.5

9. Shale, olive, silty 2.0

8. Siltstone, olive, micaceous, finely laminated in massive beds 1.8

7. Shale, olive, with numerous 1–6 inch beds of gray, argillaceous limestone and thin beds of olive, micaceous siltstone 48.0

6. Limestone, gray, in beds 2–3 inches thick, very fossiliferous, preservation poor 6.0

Total 322.8

Kathwai Member

5. Limestone, gray, glauconitic, fine-grained; contains rhynchonellid brachiopods 1.6

4. Dolomite, gray, glauconitic in upper part, weathers rust-brown 3.0

3. Dolomite, light gray, friable; contains crinoid fragments 2.6

2. Dolomite, light gray, massive, hard, weathers rust-brown; contains crinoid fragments and pelecypods 3.6

1. Dolomite, grayish tan, fine-grained 0.6

Total 11.4

Total Mianwali Formation 410.6

CHHIDRU FORMATION (Upper Permian)

00. Sandstone, grayish white 0.6

0. Limestone with abundant bellerophons

Stratigraphic section of Triassic formations exposed in Narmia Nala, Surghar Range, West Pakistan (Figs. 20, 21).

Bed No.   Thickness Feet

TREDIAN FORMATION (?Lower and ?Middle Triassic)

Khatkiara Member

Sandstone, white, massive (not measured)

Landa Member

40. Shale, black and gray, and massive dark brown to dark gray, micaceous sandstone which contains poorly preserved plant remains 100.0

Total 100.0

MIANWALI FORMATION (Lower Triassic)

Narmia Member

39. Limestone, dark gray, made up of pissolites; a conspicuous hard unit containing *Spiriferina* and other brachiopods 7.0

38. Limestone, gray, sandy, massive, weathers rust-brown, with some thin shale beds 14.0

37. Shale, gray-black, with thin beds of calcareous, fine-grained, ripple-marked sandstone 40.0

36. Limestone, gray, sandy, weathers iron-brown; contains a few ammonites (*Isculitoides* sp. indet., *Subvishnuites* sp. indet.) 2.0

35. Shale, gray-black, with thin beds of sandy dark limestone that weathers brown 22.0

34. Limestone like bed 32, contains ammonites and pelecypods 5.0

33. Shale, like bed 31 6.0

32. Limestone, light to dark gray, some beds brown, consisting of small pellets, medium-bedded; one bed filled with crinoid remains, unit contains ammonoids (*Pseudosageceras multilobatum*, *Subvishnuites* sp. indet., *Stacheites* sp. indet.), pelecypods, and orthocerids 5.0

31. Shale, gray-black, with 1–4 inch beds of fine, sandy, dark limestone that weathers brown 11.0

30. Limestone, light to dark gray, fine-grained, very glauconitic in part, medium-bedded; contains ammonites (*Arctomeekoceras* sp. indet.,
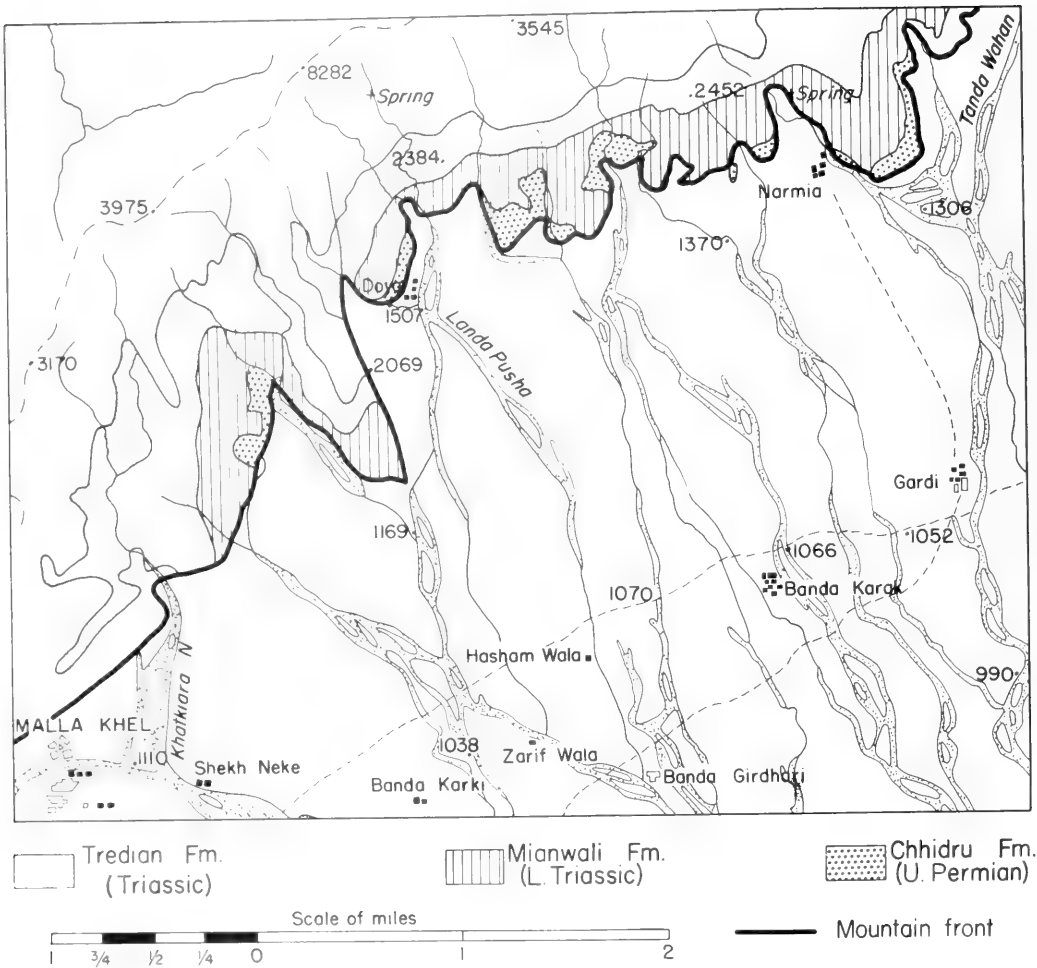
Figure 20. Locality map of Narmia and Landa region, Surghar Range, West Pakistan, showing distribution of late Permian and Triassic formations. Geologic data from unpublished map by W. Danilchik and A. Shah.

Prohungarites cf. *crasseplicatus*, *Anakashmirites* sp. indet., *Subvishnuites* sp. indet., *Xenoceltites* sp. indet., *Procarnites kokeni*, *Nordophiceras* cf. *planorbis*, *Dagnoceras* cf. *zappanense*) and pelecypods   10.0

29. Shale, olive-gray, with 10 inch bed of cross-bedded, tan, fine-grained, micaceous sandstone near top   9.0

28. Limestone, dark gray, fine-grained, very hard   6.0

27. Limestone, brown, very hard, weathers purple-brown, made up of shell fragments   1.5

26. Limestone, dark gray, weathers

iron brown, and some sandstone beds; contains poorly preserved ammonites and pelecypods   2.0

Total 140.5

Mittiwali Member

25. Shale and sandstone like bed 22   2.0

24. Sandstone like bed 21   2.0

23. Shale, black, alternating with gray sandstone in beds 1–3 inches thick   2.5

22. Sandstone, dark gray, fine- to medium-grained, massive, cross-bedded   5.0

21. Shale, black and olive gray, with intermittent beds of tan, cross-bedded sandstone like bed 20   70.0

20. Sandstone, grayish tan, cross-

bedded, in beds 2–18 inches thick, individual sand beds separated by olive shale beds 1–8 inches thick   4.0

19. Shale, olive gray, few thin beds of fine-grained, laminated sandstone   30.0

18. Limestone, gray, fine-grained, with intermittent 1–12 inch shale beds   9.0

17. Shale, olive, with thin, lenticular beds of argillaceous limestone and calcareous siltstone   15.0

16. Limestone, gray, in beds 1–4 inches thick, region of structural complexity with folds and faults   12.0

15. Siltstone, gray, calcareous, laminated, with intermittent beds of black shale   5.0

14. Limestone, gray, hard, massive, weathers tan; contains *Pseudosageceras*   1.5

13. Shale, like bed 10 but with more beds of siltstone and fine-grained sandstone, beds near top calcareous   90.0

12. Siltstone, gray, shaly in part, with interbeds of 3–6 inch beds of gray limestone and some black shale   8.0

11. Shale, black, with numerous 1–3 inch beds of laminated tan siltstone; some structural complexities in this area, thickness approximate   220.0

beds 2–4 inches thick, with a few thin shale interbeds   1.0

9. Shale, tan and gray, silty   0.2

8. Limestone, gray, argillaceous, massive, weathers tan; contains poorly preserved ammonites   1.0

7. Limestone, gray, fine-grained, weathers tan, with some thin beds of black, silty shale; contains poorly preserved ammonites   6.8

6. Limestone, gray, like bed 5, *Gyronites* common   1.5

5. Limestone, gray, medium-bedded; contains ammonites (*Gyronites*)   1.0

Total 487.5

Kathwai Member

4. Limestone, gray, hard, massive, glauconitic, no fossils seen   1.3

3. Limestone, gray, speckled brown, glauconitic   0.7

2. Dolomite, grayish tan, fine-grained, coquinoidal, consisting mainly of echinoderm fragments; uppermost foot contains glauconite   5.0

1. Limestone, grayish tan, coquinoidal, partly dolomitized; contains Permian-type brachiopods   0.5

Total 7.5

Total Mianwali Formation 635.5

Figure 21. Triassic formations in Narmia Nala, Surghar Range, West Pakistan. The strata up through the first prominent limestone bed in the middle of the photograph are the upper part of the Mittiwali Member and the Narmia Member of the Mianwali Formation. The overlying thin bedded strata are the Landa Member of the Tredian Formation, and the overlying massive sandstone beds are the Khatkiara Member.

CHHIDRU FORMATION (Upper Permian)

00. Sandstone, white, fine-grained   0.9

0. Limestone, light gray, detrital, sandy; contains productids, *Bellerophon*, and other typical Permian forms

Stratigraphic section of part of the Triassic formations exposed in Landa Nala, Surghar Range, West Pakistan (Fig. 20).

Bed No.   Thickness Feet

TREDIAN FORMATION (?Lower and ?Middle Triassic)

Khatkiara Member

20. Sandstone, white, massive

Landa Member

19. Shale and sandstone like bed 18 but more sandstone and these in thicker beds with frequent shale breaks, sandstone pink to red on weathered surface, contains ripple marks and plant fragments 27.0

18. Shale, black, with much micaceous, tan to gray to pink siltstone and sandstone in beds 1–24 inches thick ... 70.0

Total 97.0

MIANWALI FORMATION
Narmia Member

17. Limestone, gray, made up entirely of pissolites; contains *Spiriferina* and echinoid spines 4.5

16. Limestone, gray-brown, typical of sequence, with beds of thin-bedded sandstone, a few one foot shale beds, vague suggestion of pelecypods present 15.0

15. Sandstone, olive, fine-grained, micaceous, laminated 2.0

14. Shale, black with much micaceous siltstone and frequent beds of brown weathering, cross-bedded, calcareous sandstone and argillaceous limestone 29.0

13. Limestone, gray, weathers brown, with few thin shale beds, no fossils seen 3.0

12. Shale, gray, black, with thin beds of gray laminated siltstone and gray limestone, no fossils seen 21.0

11. Limestone, gray, contains poorly preserved ammonites 1.5

10. Shale, black, with some thin beds of gray, laminated siltstone 4.5

9. Limestone, gray, glauconitic, very hard; contains a few ammonites (*Pseudosageceras multilobatum*, *Anakashmirites* sp. indet., *Nordophiceras* cf. *planorbis*), orthocerids, and rhynchonellid brachiopods 7.0

8. Shale, olive, with thin beds of laminated siltstone 5.0

7. Limestone, light gray, very hard, contains poorly preserved ammonites (*Subvishnuites* sp. indet.) and pelecypods 6.0

6. Shale, black, silty in part, micaceous, with 1–3 inch beds of sandy limestone and gray calcareous sandstone 5.3

5. Limestone, light gray, fine-grained, glauconitic, medium-bedded; contains poorly preserved ammonites (*Pseudosageceras multilobatum*, *Arctomeekoceras* sp. indet., *Subvishnuites* sp. indet.) 3.5

4. Shale, black, with some thin beds of light gray, sandy limestone 1.8

3. Limestone like bed 1 .... 5.0

2. Shale, black, with some thin beds of light gray, calcareous, fine-grained sandstone 7.0

1. Limestone, gray, with brown irregular portions, fine-grained, sandy in part, with some thin beds of calcareous sandstone; contains poorly preserved pelecypods and brachiopods. This unit is believed to be equivalent to the Bivalve beds of the Salt Range 6.5

Total 127.6

Mittiwali Member

0. Section not measured in detail, first abundant fossils (*Stephanites*) occur in thin limestone beds 135 feet below the base of the Narmia Member

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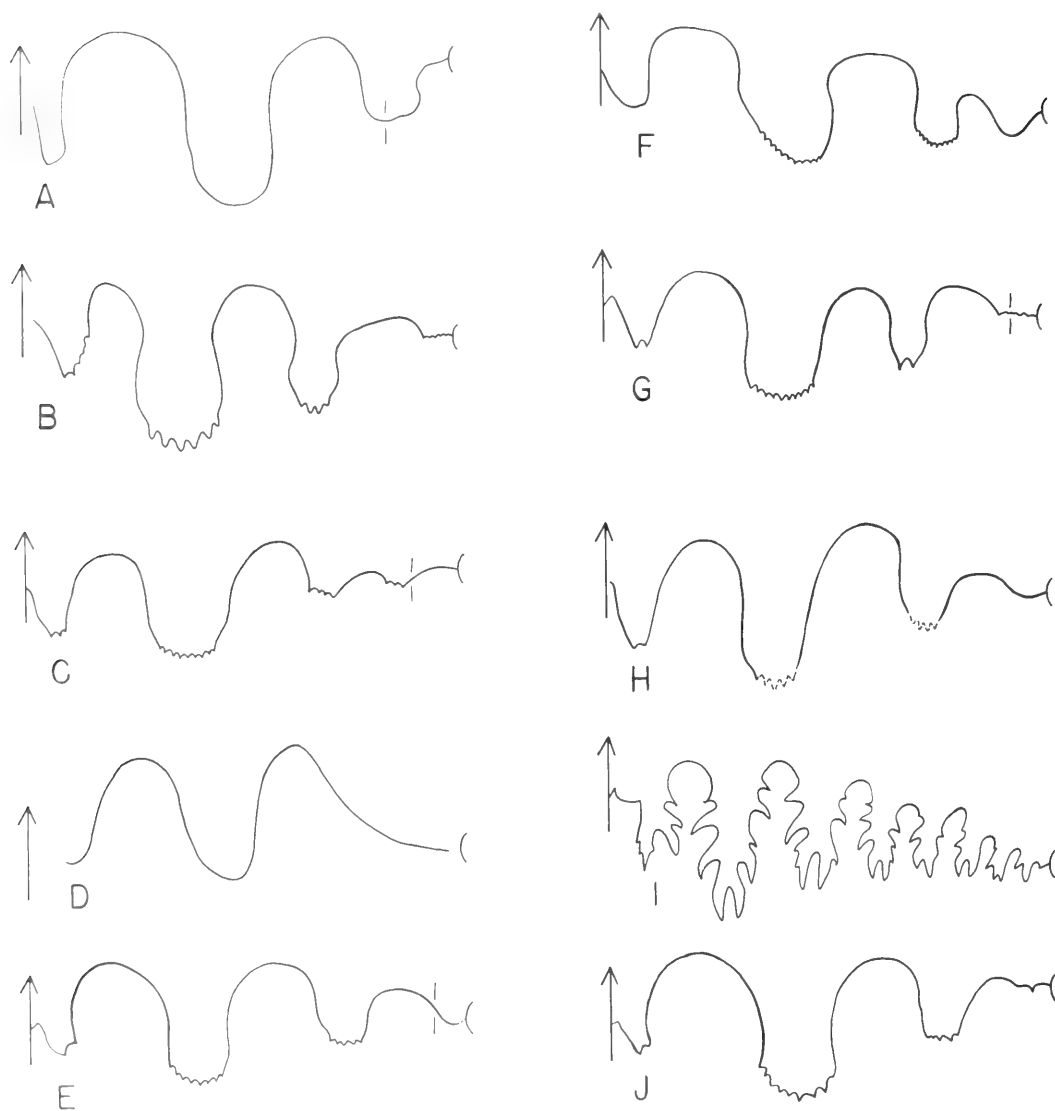
Figure 22. Diagrammatic representation of the suture of ammonites from the Narmia Member of the Mianwali Formation, Surghar Range and Salt Range, West Pakistan. A, *Dagnoceras* cf. *zappanense* Arthaber at a whorl height of 6.5 mm, MCZ 9565; B, *Nordophiceras* cf. *planorbis* (Waagen) at a whorl height of 11 mm, MCZ 9614; C, *Prohungarites* cf. *crasseplicatus* (Welter) at a whorl height of 13 mm, MCZ 9606; D, *Stacheites* sp. indet., at a whorl height of 6 mm, MCZ 9609; E, *Arctomeekoceras* sp. indet., at a whorl height of 9 mm, MCZ 9585; F, *Anakashmirites* sp. indet., at a whorl height of 9 mm, MCZ 9603; G, *Svalbardiceras* sp. indet., at a whorl height of 11.5 mm, MCZ 9587; H, *Xenoceltites sinuatus* (Waagen) at a whorl height of 15.5 mm, topotype MCZ 9581; I, *Procarnites kokeni* (Arthaber) at a whorl height of 14 mm, MCZ 9595; J, *Subvishnuites* sp. indet., at a whorl height of 7 mm, MCZ 9599.

PLATE 1.   XENOCELTITES and PSEUDOSAGECERAS

PLATE 2.   ARCTOMEEKOCERAS, SVALBARDICERAS, and PROCARNITES

PLATE 4.   NORDOPHICERAS, PSEUDHARPOCERAS, and TIROLITES

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The Taxonomy, Cytology, and Evolution of the Genus *Rhagoletis* in North America (Diptera, Tephritidae)

GUY L. BUSH

Museum of Comparative Zoology, Harvard University

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THE TAXONOMY, CYTOLOGY, AND EVOLUTION OF THE GENUS *RHAGOLETIS* IN NORTH AMERICA (DIPTERA, TEPHRITIDAE)

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THE TAXONOMY, CYTOLOGY, AND EVOLUTION OF THE GENUS *RHAGOLETIS* IN NORTH AMERICA (DIPTERA, TEPHRITIDAE)

GUY L. BUSH[1]

INTRODUCTION

The genus *Rhagoletis* (tribe Trypetini, subfamily Trypetinae) was first proposed by Loew in 1862 to include only *Musca cerasi* Linnaeus and its synonyms. Therefore, *M. cerasi* is automatically the type of the genus by monotypy.

The generic limits of *Rhagoletis* have never been in doubt except for some disagreement over the status of a group of predominantly yellow Palearctic species sometimes placed in a separate genus, *Zonosema* Loew, and the recently established genera *Microrrhagoletis* Rohdendorf and *Megarrhagoletis* Rohdendorf. These are not recognized in the present revision. However, since controversy still exists over these genera, and questions have been raised in this revision about the relationships between *Rhagoletis* and the closely related genera *Carpomyia* A. Costa and *Zonosemata* Benjamin, an attempt has been made to present as detailed an analysis as possible of the generic limits of *Rhagoletis*. Examination of Palearctic and Neotropical material borrowed from the Museum of Comparative Zoology and the U.S. National Museum, and specimens exchanged with the Leningrad Zoological Institute have made it possible to establish the relationships between various species groups with greater certainty.

The genus is widely distributed over the Holarctic and Neotropical regions and includes species that are major economic pests of fruits such as apples, cherries, walnuts, and tomatoes. Approximately 50 species and subspecies have been described, and the host plants are known for at least 42. Because of the economic importance of the genus, an extensive literature on the biology and control of certain species has accumulated over the past 100 years. One of the outstanding features emerging from these investigations is the frequent occurrence of morphologically almost indistinguishable, but apparently ecologically independent sympatric populations associated with different host plants. These populations have been variously regarded as host races, subspecies, and in some cases distinct species.

The presence of host races and sibling species in *Rhagoletis* and many other phytophagous insects has led some authors such as Brues (1924), Thorpe (1930), and Smith (1941), as well as others, to consider sympatric speciation as the most plausible explanation for the origin of many phytophagous insect species. Mayr (1963), on the other hand, contends that although host races may represent a possible case of incipient sympatric speciation, complete stabilization on a new host cannot occur without geographic isolation. However,

[1] Biological Laboratories, Harvard University, Cambridge, Massachusetts. Present address: Department of Zoology, University of Texas, Austin, Texas.

conclusive evidence in support of these hypotheses is lacking. The problem, as pointed out by Mayr, cannot be satisfactorily resolved until adequate studies are undertaken to establish the degree of reproductive isolation between different host races of the same species coexisting in the same locality.

Much of this information is already available in the economic literature pertaining to insects associated with the food crops of man. Because most of these investigations were conducted before the biological species concept was widely accepted, systematists often dismissed the results as irrelevant to the taxonomic interpretation of host races and sibling species. This early work continues to be overlooked by modern taxonomists, but the results are no less important in the interpretation of host races today than they were in the early part of the century. Most taxonomists and economic entomologists of the Tephritidae, for example, have taken a purely morphological approach in their interpretation of the differences evident in allopatric and sympatric populations associated with different hosts. For example, Benjamin (1934) and Pickett (1937), with ample biological data at hand as a result of rearing and crossbreeding experiments, considered only morphological evidence in their interpretation of host races and sibling species. This typological approach has only confused rather than clarified the status of host races of *Rhagoletis* and many other phytophagous insects.

The objective of the present revision, therefore, has been to incorporate as much of this biological information as possible into a re-evaluation of these so-called host races. Additional observations made in three years of field and laboratory work on such aspects of the problem as chromosome cytology, courtship behavior, distribution, and host relations have also been included.

The interpretation which has emerged as a result of this investigation regarding host races in *Rhagoletis* is quite different from that accepted in the past. Based on criteria established in this revision, most races appear to be distinct species and are probably oligophagous and not monophagous or polyphagous as once believed. Paleontological evidence of past plant distributions, as well as the present distribution of host plants, and of species of *Rhagoletis* currently associated with them, strongly supports allopatric speciation as a major source of new species. However, some sympatric sibling species may have become established through allochronic isolation on different hosts.

Certain aspects in the adaptation to new hosts, such as the genetics and chemistry of host selection, conditioning, and mating behavior, have yet to be studied. More thorough crossbreeding work and field studies on the ecology of this genus are badly needed. The hosts of several species are still unknown and the distribution of most species, including all those of economic importance, is yet to be definitely established.

The results presented here represent only a preliminary treatment of a very complex problem; consequently, the conclusions should be regarded as tentative. However, it is hoped that this study will furnish a basis for futher investigations.

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Additional material was collected during three summers of field work in the United States, Canada, and Mexico. These field trips were supported in part by a grant-in-aid of research from the Society of the Sigma Xi, fellowships from the National Science Foundation, and through the assistance of Harvard University. A number of individuals assisted me in locating material and in providing working facilities during the course of these field investigations. Space does not permit more than a mention of their names, but I wish to extend my sincere thanks to the following individuals: Dr. M. M. Barnes, Mr. F. L. Blanc, Mr. A. Forbes, Prof. S. C. Jones, Mr. P. Marucci, Mr. H. R. Moffitt, Mr. A. D. Pickett, Dr. M. Wasbauer, Dr. F. Werner; and members of the staff of the U.S. Department of Agriculture Fruit Fly Laboratory, Mexico City: Mr. W. Stone, Dr. F. Lopez-D., Sr. L. Torres-N., Sr. V. Torres-N., and Sr. F. E. Guiza.

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METHODS

Morphology. In order to facilitate identification of various structures referred to in the text, illustrations of the most important diagnostic characters are presented in Figures 1–16. The terminology follows that of Dean (1933, 1935), Munro (1947), and Steyskal (1957).

Chromosome morphology. The terminology in the description of chromosome morphology is that of White (1957), and Bush (1962). MCA refers to the number of major chromosome arms. Gonads and larval brain tissue were prepared for study following the method I described in 1962.

Description of color. General terms have been used to describe variation in color. Whenever possible the terminology is based on the standardized color names of the *Dictionary of Color* (Maerz and Paul, 1950). The following is a list of the color names used in the text and the code used

to designate the color in the *Dictionary of Color* which may be referred to if a more accurate interpretation is needed. Golden yellow, 915; tannish cream, 9E3; dark yellowish orange, 9L8 and 9L10; light yellowish orange, 9L4 and 9L5; yellowish orange, 9L7; brown, 7E10; lemon yellow, 9K3; tawny, 13D10; light brown, 13L10; yellowish cream, 9G2; golden tan, 10L7; golden brown, 12I8; tan, 12L10; reddish brown, 4D12.

Abbreviations used in the text. The following abbreviations are used in the lists of synonymy: ANSP (Academy of Natural Sciences of Philadelphia); AMNH (American Museum of Natural History); CNC (Canadian National Collection); CU (Cornell University); KU (Kansas University); LZI (Leningrad Zoological Institute); MCZ (Museum of Comparative Zoology); USNM (United States National Museum); GLB (Guy L. Bush).

Authorities for the botanical names are abbreviated following the form employed in the eighth edition of *Gray's Manual of Botany* by M. L. Fernald (American Book Company, New York) in the section entitled "Explanation of Abbreviated Names of Authors," pp. liii–lviii.

Locality and host data accompanying specimens. The large number of specimens examined, particularly in certain species of economic importance, has made it necessary to exclude detailed information appearing on the specimen labels.[2] Data of this nature have been summarized in distribution maps of individual species in relation to their respective hosts, and a brief résumé of pertinent features of the distribution accompanies the discussion of each species.

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[2] For those interested in detailed distribution data and in an annotated list of references, the author's Ph.D. thesis, "A revision of the genus *Rhagoletis* in North America (Tephritidae, Diptera)," may be obtained on loan from the librarian of the Biological Laboratories, Harvard University. Mimeographed copies of this information have also been placed in the libraries of the Museum of Comparative Zoology and the United States National Museum.

Lists of synonymy and other pertinent references. As previously mentioned, a great deal of literature has accumulated on certain economic and biological aspects of this genus. An attempt has been made to review all of this material except for a few strictly economic papers. Only the pertinent literature has been referred to in this revision, and the lists of synonymy have been kept as short as possible.[2]

Measurements. Certain species can only be distinguished on the basis of body measurements and indices; therefore, these must be made with accuracy. Measurements were always made by rotating the specimen until the maximum measurement was obtained. This reduced the error in measurement to a minimum by insuring that the distance between the two points being measured was at right angles to the line of vision (see Brown, 1953). All body and head measurements were made at 100× using an ocular micrometer. Wing measurements were made from slide mounted wings using a Bioscope. Structures such as the abdomen and ovipositor sheath were found to be of little use as they were distorted greatly by desiccation, thus making it impossible to obtain accurate measurements.

Measurements were made in the following way: HL—head length—measured in profile from base of antennae to base of comb; HW—head width—maximum width measured in frontal view; HH—head height—measured in profile from lower margin of genae to vertex; EW—eye width—maximum width measured in fronto-lateral view so that both lateral margins are in focus; EH—eye height—maximum height measured in a slightly dorsal and fronto-lateral view so that both upper and lower eye margins are visible; FrWV—frons width at vertex—the maximum distance between the margin of each eye measured in dorsal view along the anterior edge of the ocellar plate; AL—antennal length—measured in frontal view from upper margin of 1st segment to tip of 3rd segment; FL—face length—measured in frontal view from the peak

of the ptinial sulcus to the lower margin of the face; GW—genal width—difficult to measure accurately as the shape of the genae varies among individuals; best taken as the maximum length between the lower-most corner of the eye and the lower margin of the gena just in front of the genal bristle; TL—thorax length—maximum length measured in dorsal view from the tip of scutellum to the most anterior region of pronotum; WL—wing length—maximum distance between small break or cross sulcus in base of radial sector located just basad of junction of radial sector and humeral crossvein to end of R_{4+5}; WW—wing width—maximum width measured apicad of subcostal break.

Identification of host plants. Most of the hosts of the more common species of *Rhagoletis* were easily recognized in the field, though some could only be identified to genus. In doubtful cases, specimens were pressed and returned to the laboratory for study. Those specimens that could not be identified to species with certainty were deposited in the Gray Herbarium of Harvard University where future workers interested in host relationships may obtain an identification if specialists can be located.

Rearing. Infested fruit was placed over moist sand until all larvae had left the fruit and pupated. After two weeks the pupae, in some moist sand, were refrigerated at 4° C for two to three months. They were then removed and the sand moistened again. Usually adults began emerging within 25 to 30 days. Attempts were made to maintain the adults on a variety of diets, but the only one that proved successful consisted of powdered milk, bakers yeast, and sucrose fed in dry form. Flies had access to water at all times. Adults were permitted to live at least four days before they were pinned to insure maximum coloration and internal development.

TERMINOLOGY

Monophagy, oligophagy, and polyphagy. The use of the terms monophagous, oligophagous, and polyphagous presents special problems of interpretation. Thorsteinson (1960) maintains that a classification of food preferences in purely chemotactic terms is preferable to the more subjective system based on the number of plant species infested by an insect. While recognizing the importance of chemical stimuli in host plant selection, it is still impractical to apply this method in a discussion of host relationships in *Rhagoletis* because the chemical basis for host selection is not known. The interpretations given below have been followed in this revision.

A monophagous insect is restricted to a single species of host plant while an oligophagous insect utilizes several host species within the same genus or related genera of plants of the same family. A polyphagous species infests a wide range of host plants in several unrelated host genera of different families.

Host races and sibling species. Host races are morphologically similar or indistinguishable populations of an ecologically polymorphic species, each of which is restricted to a single host or a group of closely related hosts. As races they are not reproductively isolated from one another and gene flow can be re-established between them when ecological or geographical barriers are removed. This is in contrast to *sibling species* which have been defined by Mayr (1963) as morphologically similar or identical populations which are reproductively isolated.

In the absence of sufficient biological data, it is difficult or impossible to establish whether two or more morphologically closely related populations represent distinct sibling species or simply host races. The following "rule of thumb" was therefore used in handling this problem during the course of the present revision.

Two closely related sympatric populations associated with different host plants

and showing slight but consistent morphological differences were considered sibling species if the host plants belonged to different families or even distinct genera within a family.

The use of the host family as a criterion for establishing the status of most host races and sibling species in cases where reproductive isolation in *Rhagoletis* cannot be established seems justified on the basis of crossbreeding work conducted on members of the *pomonella* group. In this species group certain populations formerly considered only host races associated with different plant families, such as Rosaceae, Cornaceae, Caprifoliaceae, and Ericaceae, have all proved to be distinct species. Populations in the *pomonella* group associated with closely related genera within a family, however, are capable of interbreeding at least under laboratory conditions (cf. p. 455).

Morphologically distinct allopatric populations infesting either related or unrelated host plants were considered distinct species if the morphological differences between them were as great as or greater than the differences encountered between sympatric species within the same species group.

If no morphological differences could be correlated with host preference in allopatric or sympatric populations, and if the biology of the species was not well known, then the various populations associated with different hosts were considered host races.

Sympatry (Mayr, 1963). The occurrence of two or more populations in the same area. Mayr has limited this term to a population in breeding condition within cruising range of individuals of another population.

Sympatric speciation (Mayr, 1963). Speciation without geographic isolation; the acquisition of isolating mechanisms within a deme.

Allopatry (Mayr, 1963). The occurrence of populations or species occupying mutually exclusive (but usually adjacent) geographical areas.

Allopatric speciation. Speciation with geographic isolation; the acquisition of isolating mechanisms in two or more geographically isolated populations of the same species.

Syntrophic. Sharing the same or closely related food source.

Allotrophic. Utilizing different food sources.

Allochrony. The occurrence of conspecific populations or species in breeding condition (e.g., host races) at different times of the year.

Allochronic speciation. Speciation by temporal isolation. The acquisition of isolating mechanisms in two or more allochronically isolated populations.

BIOLOGY OF THE GENUS *RHAGOLETIS*

A complete review of the biology of *Rhagoletis* will not be attempted here. Reference may be made to Illingworth (1912), O'Kane (1914), Porter (1928), Nicholson (1929–30), Lathrop and Nickels (1932), Boyce (1934), Pickett (1937), Wiesmann (1937), and Christenson and Foote (1960) for further details. A few salient features of the biology should be mentioned, however, as they not only have a direct bearing on the population structure and evolution of the flies themselves, but also offer clues that may be used to interpret the status of the many host races recorded in this genus.

Larval food habits. As far as is known, the larvae of all species feed in the fleshy pulp of fruits and berries. Based on the criteria used in this revision to denote the degree of host specificity, all species are probably oligophagous, being restricted to a narrow range of closely related hosts. None that have been carefully studied were found to be either monophagous or polyphagous as previously reported by some authors. Although oligophagous, most species show a definite preference for certain host species within a genus, or even for

particular varieties of a single species (Illingworth, 1912; O'Kane, 1914; Wellhouse, 1920; Lathrop and Nickels, 1932).

Host transfer experiments. Most of the sibling species formerly considered host races show some minor morphological differences, particularly in overall size and in the structure of the genitalia. Some authors have attributed these differences either to nutritional qualities of the various hosts or to geographic variation (Benjamin, 1934; Pickett, 1937; Hall, 1938). Host transfer experiments conducted by several investigators indicate that genetic factors may also be involved. Lathrop and Nickels (1932) found that first and second instar larvae of *R. mendax* from blueberries would complete development when placed in apples, but the resulting pupae and adults were of the normal small size typical of the blueberry form. When *R. pomonella* from apples was transferred to blueberries, or induced to oviposit in this fruit, the resulting pupae and adults were of normal size for the apple form. This would indicate that in these two reciprocal host transfers the genotype and not the food supply determined body size.

Nutrition and crowding seem to influence adult size in some instances. Hall (1938) reported that pupae and adults resulting from the forced oviposition by *R. pomonella* in *Cornus* berries were smaller than normal, suggesting a nutritional effect on body size. It does not follow, however, that the sibling species, *R. cornivora,* which infests *Cornus,* is smaller because of a nutritional deficiency in its host fruit. Reciprocal infestation of *R. cornivora* in apples was not made, as the adults refused to oviposit in the fruit. The small size of both *cornivora* and *mendax* undoubtedly has some adaptive function that has not been determined as yet.

In the *suavis* group where many females may oviposit on a single walnut, crowded conditions may result in abnormally small adults (see *Hosts, R. completa*). In other species groups, more than one larva in a

fruit is rare (except in the case of infestations in large fruits such as apples). Multiple oviposition in these species is apparently inhibited by a pheromone laid down by the female prior to oviposition (Hafliger, 1953).

Diapause and emergence. All Holarctic species of *Rhagoletis* that have been studied are essentially univoltine, with the adults of various species emerging at different times during the summer. Usually, diapause must be broken by a period of low temperature, some individuals requiring as many as four successive chillings in as many years before they complete development (Boyce, 1934). At least one Neotropical species, *R. lycopersella* Smyth which infests tomatoes in Peru, apparently is adapted to arid conditions. Its diapause can be terminated by simply placing pupae in a moist environment (Smyth, 1960). These characteristics are of considerable selective advantage as they insure a supply of adults every year even though the host in a given area fails to bear fruit for several consecutive seasons.

Emergence generally occurs over a relatively short period with 60–90 per cent of the flies emerging within two to four weeks. This emergence is synchronized with the maturation of the host fruit and usually never varies more than two weeks from year to year. A few flies, however, emerge up to a month before and after the peak emergence period. These early and late emerging flies are at a considerable selective disadvantage, and a substantial number probably perish without leaving progeny since host fruits are not readily available for oviposition. They do, however, insure the presence of some flies to maintain a resident population in years when for some reason peak emergence does not coincide with host maturation. The rare occurrence of such an event in any one area possibly accounts for the low frequency of these "off season" flies in natural populations. They may also play an important role in the

formation of new host races and species through allochronic speciation (p. 447).

The factors controlling diapause in the North American and European species are not well understood. The close adaptation of various species to the fruiting times of their respective hosts would indicate that emergence periodicity is under genetic control and is probably regulated by certain components of the environment, such as temperature and day length.

Illingworth (1912), Hall (1938), and others have noted a small second brood in *R. pomonella*. A few adults may emerge late in the summer or early fall from larvae that pupated the same year. Hall (1938) observed that second brood adults emerging in the same summer in which they pupated were obtained in Ontario only from pupae formed before August 20. This suggests that light (day length), temperature, or both, may influence emergence by acting in some way on the host plant or on the previous generation of flies. Diapause may, therefore, be facultative and not obligatory, at least in some individuals.

Normally these flies would find few fruits in which to oviposit, and it is unlikely that their larvae, if any are produced, could complete development before freezing temperatures set in. A second brood may be important in the southernmost part of the range of certain species of *Rhagoletis* where host maturation is spread over a longer period and where freezing temperatures occur infrequently. But in these areas there is no indication as yet of a regular second brood.

Adult longevity. Adults are known to live up to 70 days in the laboratory, but it is doubtful that many ovipositing females survive for more than 20-30 days under natural conditions.

Flight range and dispersal. Recent investigations using radioactively-labeled flies demonstrated that *R. completa* is capable of dispersing up to one mile in 21 days and probably farther under favorable conditions (Barnes, 1959). Studies on other Tephriti-

dae, such as *Dacus dorsalis* Hendel, *Ceratitis capitata* (Wiedemann), and *Anastrepha ludens* (Loew), indicate that these flies are capable of covering considerable distances over unfavorable areas (Christenson and Foote, 1960). *A. ludens*, for instance, is known to travel 160–175 miles from the nearest breeding areas in northern Mexico to southern Texas. Prevailing winds are apparently the most active agents in dispersal. Distance and unfavorable terrain, therefore, cannot always be considered absolute barriers to dispersal. Normally, however, adults of *Rhagoletis* do not disperse rapidly if suitable hosts are available, but congregate in trees which bear fruit in suitable condition for oviposition.

Mating behavior and territoriality. Courtship in most species of *Rhagoletis* that have been observed relies heavily on visual cues. Males court and females respond to courtship with various movements of the wings and body which are adorned in both sexes with contrasting color patterns. Use of the wings in courtship displays may account for the widespread occurrence of distinctive species specific and occasionally sexually dimorphic wing patterns in many groups of Tephritidae.

Sexual dimorphism in color pattern of the body is found in two widely separated *Rhagoletis* species groups. Three of five species in the *suavis* group show varying degrees of differences in thorax and abdomen coloration, the males being much more heavily pigmented with black than the females. In the *ribicola* group, the legs of *R. ribicola* males are entirely yellow. Only the front pair of legs in the female are yellow, while the other two pairs are dark brown. These patterns apparently play a role in sex and species recognition.

The fact that males of *R. completa* respond to certain chemical lures (Barnes and Osborn, 1958) also suggests that chemical releasers play some as yet undetermined role in courtship. Pheromones are known to be used as sex attractants by females of some species of Tephritidae (Christenson

and Foote, 1960), and Féron (1962) has shown that, at least over short distances, males of *Ceratitis capitata* also produce a sex attractant during the initial stages of courtship. It would not be surprising to find similar pheromones in other tephritids as well.

However, both sexes of many species of *Rhagoletis, Anastrepha,* and other tephritid genera respond to certain fermenting and chemical lures (Christenson and Foote, 1960). These apparently do not simulate sex pheromones, but seem to mimic odors produced by either a suitable food supply or oviposition site. This suggests that certain odors emitted by host plants may function as secondary sex attractants since they bring the two sexes together on a common host or food source. This is apparently the case in *Rhagoletis* and many other tephritids where mating occurs on or near the host plant. Plant odors may therefore be particularly important as a rendezvous stimulus in those groups of Tephritidae that rely primarily on visual releasers in courtship in the absence of long distance chemical or auditory unisexual sex attractants.

Auditory releasers commonly used in courtship by species of *Dacus* (Monro, 1953; Browne, 1957b) and *Ceratitis* (Féron, 1960) have not been demonstrated in any species of *Rhagoletis.* However, there is some indication that light intensity influences courtship as it does in *Dacus tryoni* (Froggatt) (Browne, 1957a) and *Ceratitis capitata* (Féron, 1957). In *R. completa,* courtship and mating are most frequently observed in the late afternoon (Boyce, 1934).

The fact that courtship and mating occur on the host plant means that there is little chance for sympatric allotrophic populations of host races and sibling species to encounter one another during this critical phase in their life cycle. Therefore, the restriction of mating to the host plant has important implications in the formation of host races and speciation.

Males of the *suavis* group are known to

be territorial, and there is good evidence to suggest that the other species of *Rhagoletis* also maintain temporary or "floating" territories consisting of a single fruit or a cluster of fruits.

Host specificity and oviposition behavior. Evidence has been presented which indicates that under both laboratory and field conditions many species of *Rhagoletis* are capable of ovipositing in a wide range of fruits which are not their normal hosts. In some cases, mature larvae and even adults of a particular species have been reared in the laboratory from hosts that are never found infested by the species in the field. For example, Pickett (1937), and Pickett and Neary (1940) were able to induce *R. pomonella,* a species infesting several genera of Rosaceae (Table 6), such as haw (*Crataegus*), apple (*Pyrus*), and plum (*Prunus*), to oviposit in such fruits as blueberry (Ericaceae) and snowberry (Caprifoliaceae). Other genera in the Rosaceae that are not normally considered hosts, i.e., pear (*Pyrus*), mountain ash (*Sorbus*), and sweet cherry (*Prunus*), were also artificially infested by *pomonella.* In addition to these oviposition records, Hall (1938) was able to induce *pomonella* to oviposit in tomato (Solanaceae) and *Cornus amomum* (Cornaceae). Mature larvae developed in all these fruits, but the number recovered was usually abnormally low. With the exception of pear and mountain ash, all of these plants are hosts for other species of *Rhagoletis,* some very closely related to *pomonella.*

Even under natural conditions, these flies are not host specific in their oviposition habits. Glasgow (1933) found that *pomonella, cornivora,*[3] *tabellaria, cingulata,* and *fausta* regularly oviposited in the fruits of 30 out of 39 species of fruit-bearing plants growing in the vicinity of infested apple and cherry trees. Of these 30, only 15 served as normal hosts while the remaining

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[3] Glasgow did not recognize *R. cornivora,* but considered the *Cornus*-infesting form to be *R. pomonella.*

15 were apparently unsuitable for larval development. Although eggs and larvae were frequently found in these non-host fruits, adults were never reared. Glasgow concluded that the *Rhagoletis* under study were somewhat lacking in discrimination in their egg laying habits, and undoubtedly oviposited in many fruits in which there was no possibility of the species surviving.

But indiscriminate oviposition may not be the whole answer. Often the female will pierce the fruit of both host and non-host species with her ovipositor but deposit no eggs. Instead, she will turn and feed on the exuding fruit juice. Even when eggs are deposited, the female may often feed in a similar manner (Doane, 1898; Boyce, 1934; Tominic, 1954). Oviposition and pseudo-oviposition (when eggs are not deposited) in some cases may therefore function as a means of acquiring necessary nutrients.

The non-host fruits involved in pseudo-oviposition are also not as indiscriminately selected as Glasgow assumed. Of the 15 species of non-host plants in which oviposition occurred, 13 belong to genera, and sometimes even represent the same species, infested by other *Rhagoletis* species. There may be some component of the plant or fruit which either mimics the normal host plant or furnishes something needed by the female in her diet. The habit of selectively ovipositing in what are normally non-host species may also account for the fact that species of *Rhagoletis* from widely separated groups have independently become adapted to the same genera and sometimes the same species of plants. If a fortuitous mutation or recombination permits larvae to survive in the new host, a new host race may eventually become established.

To my knowledge, the genetics of host selection and the ability to survive in any given host has not been established for any species of phytophagous insect. The ability of many tephritids to rapidly establish host races on introduced plants, however, would indicate that only minor shifts in the genotype are required in some cases.

Distribution of Rhagoletis in relation to host plants. It might be expected that by now the distribution of such economic pests as *R. pomonella, R. cingulata,* and *R. completa* would be fairly well established, but unfortunately this is not the case. However, enough is known to indicate that most, if not all, species do not cover the entire range of their hosts. Although the various species are ultimately dependent on their host plants, other factors seem to restrict their distribution. Thus, in many cases host plants may be continuous over most of North America, but the *Rhagoletis* associated with them can be found only in certain parts of the host range.

With the exception of the *suavis* group and possibly several Neotropical species, all other *Rhagoletis* species are restricted to fairly temperate mesic conditions with substantial rainfall and seasonal change. None of the northeastern species of *Rhagoletis* whose hosts extend more or less continuously over northern United States and southern Canada, are able to penetrate much beyond the 100th meridian. Even those species of the *suavis* group found in semi-arid regions of Mexico and southwestern United States are associated with walnuts growing in moist conditions along stream beds or at high altitudes. Most species, therefore, appear to be less tolerant than their hosts of dry conditions. This factor has probably played a major role in limiting the distribution of many species. Slight climatic changes could leave isolated pockets of flies even though the distribution of the host remained more or less continuous. These populations of flies, if isolated for a sufficient period, could be a source of new species and could have some influence on the evolution of a temperate climate genus such as *Rhagoletis.*

Geographical variation. Two morphological trends associated with latitude have been noted in several *Rhagoletis* species. There is a tendency toward an overall reduction in size at the more southern limits of the range of such wide-ranging species as *pomonella, completa,* and *cingulata.* A sec-

Table 1. The probable origin and current distribution of North American *Rhagoletis* species groups. Host families indicated in parentheses.

North American Origin		Eurasian Origin or with Eurasian Affinities		Central or South American Origin	Origin Uncertain
East	N West	East	N West	East, S West and Mexico	N East and N West
POMONELLA GROUP		**TABELLARIA GROUP**		**SUAVIS GROUP**	
pomonella (Rosaceae)	*zephyria* (Caprifoli-aceae)	*juniperina* (Cupressa-ceae)	*juniperina* (Cupressa-ceae	*suavis* (Juglandaceae)	*fausta* (Rosaceae)
mendax (Ericaceae)		*tabellaria* (Cornaceae)	*tabellaria* (Ericaceae)	*completa* (Juglandaceae)	
cornivora (Cornaceae)			*persimilis* (host ?)	*juglandis* (Juglandaceae)	
			ebbettsi (host ?)	*boycei* (Juglandaceae)	
				zoqui (Juglandaceae)	
CINGULATA GROUP		**RIBICOLA GROUP**		**STRIATELLA GROUP**	
cingulata (Rosaceae)	*indifferens* (Rosaceae)		*ribicola* (Saxifraga-ceae)	*striatella* (Solanaceae)	
osmanthi (Oleaceae)			*berberis* (Berberi-daceae)		
chionanthi (Oleaceae)					
		ALTERNATA GROUP			
		basiola (Rosaceae)	*basiola* (Rosaceae)		

ond trend also found in these southern populations is a reduction in the extent of dark brown and black pigmentation. This is particularly apparent in *cingulata*. The reasons for these trends are not known.

THE ORIGIN AND EVOLUTION OF NORTH AMERICAN *RHAGOLETIS*

Geographical aspects of intrageneric relationships. The predominantly Palearctic *alternata* species group and also most of the Neotropical species show several close morphological affinities which may be considered primitive. They have the wing vein R_{4+5} setulose, and have retained the same basic wing pattern and head shape. The present disjunct distribution of species bearing these features, as well as the presence of these characters in other closely related genera such as *Zonosemata, Carpomyia,* and *Rhagoletoides,* suggest that they were present in the early stages of development of *Rhagoletis.* Although similar in these basic characters, the *alternata* group and Neotropical species have diverged considerably in other features, such as the shape of the spermathecae, and in their host relationships.

The more specialized members of the genus are concentrated in eastern North America and the Palearctic region, particularly in eastern Asia. Species from these regions bear few or no setae on R_{4+5}, and show a considerable variation in wing pattern and, to some extent, in head shape. As shown in Table 1, most of the North American representatives of the genus have originated from these two centers of secondary radiation which were probably established after the original dispersal of *Rhagoletis*.

Although the Neotropics has been a major center in the development of new species, it has furnished only *R. striatella* and possibly members of the *suavis* group to the North American region. Only one of these, *R. suavis*, has been able to reach the eastern part of the United States, and none has penetrated into the Northwest, which has been floristically cut off from Mexico since the Middle Pliocene (Axelrod, 1958). Since no members of the *suavis* group occur in native California species of walnuts but are found in Arizona and New Mexico, it is likely that this species group either did not become established on walnuts or did not reach Mexico and the Southwest until at least after the early Pliocene.

Historical aspects. The time and place of origin of the genus *Rhagoletis* are not known. The fact that most of the species are adapted to high altitudes or a temperate climate supports the Holarctic region as the most probable original center of radiation. There is no fossil record of any Tephritidae,[4] although fossils of the closely related family Otitidae have been described from the Miocene Florissant shales of Colorado (Cockerell, 1915, 1916, 1917; Melander, 1949), and appear in the Oligocene Baltic amber (Loew, 1864). It is possible that tephritid representatives existed during or

before this time, but the large number of species in this family which infest the heads of composites, most belonging to the subfamily Tephritinae, could not have arisen much before the Miocene. Fossil pollen representing the earliest record of the large diversified plant family, Compositae, is not known before the lower Miocene (MacGinitie, 1958). The fruit-infesting forms could have arisen considerably earlier, as fossils of genera now infested by *Rhagoletis*, for instance, are frequently found in Cretaceous deposits.

As far as I have been able to ascertain, however, acalypterates have never been described from the Cretaceous, and do not appear until the Eocene. Furthermore, evidence provided by the past floristic history of the Holarctic region and the present distribution of *Rhagoletis* indicates that the genus, as well as most other tephritid genera, arose sometime in the Oligocene or early Miocene.

It is now well established that a continuous temperate climate flora, usually referred to as the Arcto-Tertiary geoflora, existed until the late Eocene over the entire Holarctic region (Chaney, 1947; Axelrod, 1958). The northern elements of this flora were coextensive from Eurasia to western and, in some cases, eastern North America until the late Pliocene or Pleistocene break in the Bering land bridge. For some of the more southerly members of the flora, a climatic barrier has probably existed since Miocene times (Chaney, 1947).

Although this Miocene break may have occurred after the Tephritidae became established, it has apparently influenced the distribution of at least one subfamily.[5] The Dacinae, whose members infest the fruits of various tropical and subtropical plants, probably originated during or after the Miocene break as it is presently widely represented in the Old World tropics and

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[4] Cockerell (1924) erroneously placed his *Eophlebomyia claripennis* from the Green River Eocene shales of Colorado in the family Tephritidae. This has since proved to be more closely related to the *Glossina*, and is definitely not an acalypterate (Cockerell, 1925).

[5] The distribution of the related family, Richardiidae (superfamily Tephritoidea, see Steyskal, 1961), which is restricted to tropical and subtropical America, indicates that this family also may have arisen after the Miocene break.

Australia but has only one highly specialized and aberrant genus, *Toxotrypana* Gerstaecker, in the New World.

Rhagoletis and other temperate climate genera, on the other hand, probably followed their host plants across the Bering land bridge whenever conditions were favorable during the late Tertiary and certain parts of the Quaternary. One host plant of *Rhagoletis*, *Rosa acicularis* Lindl., is still coextensive over Eurasia and North America (Lewis, 1959), and is infested by the Palearctic and Nearctic sibling species, *R. alternata* and *R. basiola*. In western North America, other hosts of *Rhagoletis*, such as *Mahonia, Juniperus, Ribes*, and *Vaccinium* of the subgenus *Euvaccinium*, have very closely related species or conspecific representatives in Eurasia or eastern Asia. All of these genera are infested by *Rhagoletis* belonging to Eurasian-centered species groups which probably entered western North America in the late Pliocene or Pleistocene.

Floristic connections between eastern and western North America, and between the West and Mexico, however, have not been continuous throughout the Cenozoic. Climatic changes initiated in the Lower Eocene established a barrier which by the Oligocene prevented the migration of floristic elements either southward into Mexico or eastward. This barrier existed well into the Miocene, during which time there was little exchange of plant species from the East to the Northwest, or between the West and Mexico.

Contact was evidently re-established between the East and West in the Upper Miocene, probably through southern Canada (MacGinitie, 1958). During the Upper Miocene, and possibly the early Pliocene, there was also some floristic interchange between Mexico and western North America, but apparently arid conditions prevailing in what is now Texas prevented a free interchange of species between Mexico and eastern North America (Dressler, 1954). It was probably during this time that *Rhago-*

letis penetrated southward into South America via a route through western North America.

Although land connections between North and South America were not established until the late Pliocene or early Pleistocene (Lloyd, 1963), hosts of *Rhagoletis*, such as *Juglans* and many of the solanaceous plants, were probably available for colonization long before continental connections were established. Considering the known ability of the Tephritidae to cover long distances over inhospitable terrain and water gaps, it is very likely that the many islands between Central and South America present during parts of the Cenozoic offered suitable steppingstones for dispersal.

Contact between the floras of Mexico and the West, and between the East and the West, did not exist for long as the cooling and drying trend that characterized the late Cenozoic soon replaced the subtropical scrub of the central plains area with the modern herbaceous vegetation. In the Northwest the cool dry climate of the Pliocene forced the Arcto-Tertiary geoflora both coastward and farther southward. This resulted in a disjunct east–west distribution in some genera. The dry summer climate of this period in North America also led to the disappearance from the West of a great many broad-leaf deciduous genera, including *Juglans*, which survived in eastern North America.

It is possible that some of the present sibling species pairs such as *R. pomonella–R. zephyria*, and *R. cingulata–R. indifferens* were established during this period of the Pliocene, although a later date is more likely. There was ample opportunity during the interglacial periods of the Pleistocene for such hosts as *Prunus, Cornus, Symphoricarpos, Crataegus*, and *Vaccinium* to re-establish contact through southern Canada and northern United States as they have done since the last glaciation. The Pliocene was, therefore, probably a time of extinction rather than generation

for many *Rhagoletis* species in the Northwest as their host plants disappeared.

This period also probably marks the time when the originally widespread *Rhagoletis* fauna was broken into at least three major groups, one in Asia, another in eastern North America, and a third in Central and South America. The present distribution of *Rhagoletis* supports this conclusion. A comparison of the native northwestern species with those of Eurasia and eastern North America (Table 1) shows that this region has no autochthonous species groups. All of its species have been either derived from the East or from Eurasia. Nor are there any known autochthonous sibling species in this region, a feature common to the Eurasian and northeastern species of *Rhagoletis*. Some of the species are, however, members of allopatric sibling species pairs with the other member of the pair in Eurasia or the Northeast.

Major physiographic and climatic changes in the late Pliocene and Pleistocene brought about a new reshuffling of the floristic elements between the East and West, and for the first time between the East and Mexico. During this period few, if any, connections were established between Mexico and the West. This was a time when much of the Rocky Mountain chain of western North America and the Sierra Madre Oriental of eastern Mexico were uplifted, and when four successive waves of glaciation caused repeated drastic shifts of the temperate flora (Dressler, 1954; Flint, 1957). When floristic connections between Mexico and eastern North America were established during the pluvial periods of glaciation, certain mesophytic and xero-mesophytic representatives of the eastern temperate forest probably entered Mexico through the Big Bend region of Texas. Once in Mexico, they were able to survive in the newly formed mountains during the warm, dry interglacial periods (Dressler, 1954; Sharp, 1953). While floristic connections existed between Mexico and the East, *R. pomonella*, belonging to a group

centered in the East, probably penetrated into Mexico along with or following its host plant *Crataegus*. *R. suavis* and *R. completa*, both members of a predominantly Mexican-centered group, apparently also entered the East at this time either with *J. nigra* or when connections were established between Mexican *Juglans* and *J. cinerea* through expansion of their ranges.

The southeastern part of the United States also underwent drastic changes. The accumulation of the earth's water in the form of ice during glacial periods resulted in a drop in sea level exposing much of the now submerged gulf coastal plain. The interglacial periods, some of which were warmer and apparently drier than the present, brought about a subsequent rise in sea level which inundated the gulf coastal plain and left parts of Florida exposed as islands or small island archipelagoes. Presently associated with these former islands in Florida are many species and distinct races of plants and animals that had their origin as isolated populations during these interglacial periods (for summary see McCrone, 1963, and Howden, 1963).

Some of the species of *Rhagoletis* now restricted to the Southeast probably had their origin on these islands during the Pleistocene. The hosts of *R. osmanthi* and *R. chionanthi*, for example, are among the plants which have distinct subspecies presently associated with these former islands and offer an explanation for the apparently recent origin of these two sibling species of *Rhagoletis* in the Southeast.

Some of the southeastern as well as northeastern plants, such as *Osmanthus americanus*, *Cornus florida*, *Vaccinium arboreum*, and *Prunus serotina*, also have isolated populations in Mexico which are not known to be infested by any species of *Rhagoletis* associated with these plants in the East. If a careful search fails to locate these eastern species in the potential Mexican host populations, it will lend fur-

ther support for a recent origin of many eastern species of *Rhagoletis*.

Speciation in the genus Rhagoletis. Allopatric speciation is probably the most common pattern of evolution in *Rhagoletis* and may result in two quite distinct end products, depending on the initial degree of host specificity (or ecological amplitude) of the parent species.

The first involves divergence of two isolated populations of a species on the same or closely related host. This is best illustrated in the *suavis* group whose species normally infest only walnuts (*Juglans* spp.). Evidence of the past movements of *Juglans* (McVaugh, 1952; Manning, 1957) indicates that there was ample opportunity prior to and during the Pleistocene for allopatric speciation on isolated populations of walnuts. If contact between these populations was re-established through expansion of the range of their host plants or chance long distance dispersal, competition on the same host would be intense and, since mating in this genus occurs on the host plant, the chances for hybridization would be high. If there had been sufficient divergence in isolation, selection would favor adaptations increasing the frequency of homogamic matings.

Characters associated with visual releasers, which are important components of courtship displays and species recognition in this genus, have been exploited by the *suavis* group in the course of establishing isolating mechanisms. Each species has a distinctive wing pattern and body coloration, and three of the five species in the group show varying degrees of sexual dimorphism. Other adaptations, such as altitudinal preference and difference in emergence times, have also helped to reduce interspecific competition (see *Hosts* of *R. boycei*).

Geographic isolation in other species groups, however, has involved a shift to an entirely new host without a corresponding shift in characters associated with courtship behavior. Courtship and mating

in these groups would occur on different hosts, thus reducing the chance of hybridization. Competition for oviposition sites would, therefore, be negligible, and as a result, the need for the development of isolating mechanisms associated with visual releasers would be greatly reduced. Perhaps for this reason sibling species are found only in those groups whose members have widely different host preferences.

A shift to a new host could come about in two ways. A species with both primary and secondary hosts may become isolated on the secondary host in a locality where climatic changes lead to the slow extinction of its primary host. The species would then be left to specialize on the secondary host, and, in time, would diverge sufficiently so that it would be unable to utilize the original host, or would be competitively excluded from it by the presence of the parent species when contact is re-established. Such a pattern could have been followed in several groups of *Rhagoletis* which now have allopatric sibling species associated with different hosts in the eastern and western parts of North America (i.e., *pomonella* and *zephyria*, *cingulata* and *indifferens*, and possibly *tabellaria* on *Vaccinium* and *tabellaria* on *Cornus*).

A second possibility, suggested by Mayr (1963, p. 462), involves a shift from a primary to a secondary host in temporarily isolated peripheral populations before the original host is entirely extinct. Adaptation to the new host under these conditions could be rapid. It could also account for sympatric sibling species encountered in certain species groups of *Rhagoletis* (i.e., *pomonella, mendax,* and *cornivora* in the *pomonella* group; *cingulata, osmanthi,* and *chionanthi* in the *cingulata* group).

Although allopatric speciation can satisfactorily account for the origin of all sympatric sibling species in this genus, a second pattern of evolution involving allochronic speciation is also open to certain univoltine phytophagous species with rather narrow host requirements (Smith, 1941). Special-

ization on a few host plants has the advantage of reducing interspecific competition, but also means that the species must be more closely attuned to the seasonal cycle of the host than would an insect infesting a wide range of plants.

In a cold temperate region, plants have definite flowering and fruiting times. Most *Rhagoletis* species must emerge at a certain time each year to insure the presence of the greatest number of suitable oviposition sites. It is not surprising, therefore, that many univoltine phytophagous insects in a temperate climate have relatively sharp peaks of abundance during the summer months. A few flies, however, emerge as much as a month early or late during periods when the host is not generally available for oviposition. This habit of early and late emergence, coupled with the fact that many *Rhagoletis* species oviposit freely in non-host plants, could greatly facilitate allochronic speciation which might occur in the following way.

If eggs are deposited and larvae are able to develop in a non-host native plant, or one that has been recently introduced, a population may become established on the new host. At least three alternatives are open to this population. (1) If the optimum stage for oviposition and larval development of the new host coincides with that of the old host, the species may simply expand its ecological amplitude to include the new host, or (2) it may become an ecologically polymorphic species with distinct host races (Ludwig's theorem, see Mayr, 1963). (3) If the stages of development of the new host and old host do not coincide, the resulting population on the new host may build up to such large numbers in relative isolation that gene flow between the two populations, if it does occur, is greatly reduced or negligible. This would permit the new population to adapt itself rapidly to the new host. The degree of allochronic isolation would naturally regulate the amount of gene flow,

which is the critical factor in determining the rate and degree of divergence.

It should be pointed out that for two allochronic populations to become established it would not be necessary for the initial infestation on the new host to be temporally isolated from the parent population. A small population could first become established on a few late maturing varieties of the new host. Selection would then favor flies with genotypes associated with early emergence, as early emerging flies would find a more abundant host supply available for oviposition. This shift would probably occur rapidly and end when peak emergence coincided with the peak maturation period of the new host. The net result would be exactly the same as in the case where the original population became established from early emerging flies.

There is now some evidence that, under certain conditions, host races and even species of phytophagous insects may be formed in a relatively short period of time (Smith, 1941; Andrewartha and Birch, 1954; Zimmerman, 1960; Mayr, 1963). Rapid host race formation has occurred in several *Rhagoletis* species within the last hundred years, probably through allochronic isolation.

There is fairly good evidence that the apple race of *R. pomonella* originated about 1860 in the Hudson River Valley from a *Crataegus*-infesting population (see *Hosts of R. pomonella*), and within 40–50 years spread west to Minnesota, south to North Carolina, and northeast to Nova Scotia (Illingworth, 1912; O'Kane, 1914; Porter, 1928). The apple race now shows a decided preference for fragrant summer and fall varieties of apples, and, although early reports record infestations in late maturing varieties, it is now rarely recovered from such fruits (Illingworth, 1912; O'Kane, 1914; Dirks, 1935). Today, the varieties preferred by the apple race mature considerably earlier than do the fruits of *Crataegus* infested by the haw form, but

the amount of overlap between the times of emergence of the two has never been accurately established.

The first population on apples may have originated from only a single pair of early emerging flies from a local haw population, or could also have occurred via one or more females from the haw population ovipositing in late apples followed by a shift in emergence to coincide with the time of greatest fruit abundance.

A similar shift to a new host is presently occurring in the California population of *indifferens* whose normal host is *Prunus emarginata,* or pin cherry. This plant grows in great abundance in northern California and is heavily infested with the western cherry fruit fly. The cultivated cherry, which matures much earlier than the pin cherry, is normally not infested. A cherry orchard may be completely surrounded by pin cherry but remain entirely free from attack by this fly. Occasionally, however, late maturing cultivated cherries may be infested by early emerging pin-cherry flies. The California State Department of Agriculture's effective eradication program has never permitted these newly established populations to build up. Without continued surveillance, it is very likely that a permanent population of *indifferens* associated with cultivated cherries would rapidly become established as it has in Oregon and Washington.

The possibility of two species arising sympatrically from a single population of flies, therefore, is a definite possibility and needs further investigation. The importance of reducing gene flow between the two host races cannot be overstressed. Without a drastic reduction of gene flow, it seems unlikely that isolating mechanisms could be established readily. Just how drastic the reduction of gene flow must be naturally depends on the intensity of selection.

It should be noted that allochronic speciation and race formation probably would not be open to many tropical or subtropical phytophagous insects since annual periodicity, at least in the Tropical Belt, is often extended over longer periods of time (Richards, 1952), and insects are usually multivoltine. Secondary hosts are almost an absolute necessity for these tropical species. This may explain why tephritids capable of infesting a multitude of host plants are restricted to tropical and subtropical regions. Apparently it is most advantageous for the univoltine, temperate climate species to become specialists. Host diversity in tropical representatives of Tephritidae is probably more greatly influenced by interspecific competition than by the ability to survive in other hosts.

Genus RHAGOLETIS Loew

Rhagoletis Loew, 1862, Europ. Bohrf., p. 44. [Monotypic; type (not examined, location unknown): *Musca cerasi* Linnaeus.] —Coquillett, 1910, Proc. U.S. Nat. Mus., 37: 599 (type, *Musca cerasi* Linnaeus). —Bezzi, 1911, Boll. Lab. Zool. Portici, 5: 14–15 (key to species, bibliography). —Hendel, 1927, *In* Lindner, Flieg. Pal. Reg., 5: 20, 74 (key to Palearctic species, description). —Cresson, 1929, Trans. Amer. Ent. Soc., 55: 401–404 (key to North American species, description). —Curran, 1932, Amer. Mus. Nov., 526: 3–4 (key to North American species, description). —Aczél, 1954, Dusenia, 5: 75–78 (description, key to Neotropical species). —Rohdendorf, 1961, Ent. Obozr., 40: 176–201 (key to Palearctic species).

Zonosema Loew, 1862, Europ. Bohrf., p. 43. Two species included; type species (not examined) = *Trypeta meigenii* Loew, designated by Coquillett, 1910, Proc. U.S. Nat. Mus., 37: 622. —Rohdendorf, 1961, Ent. Obozr., 40: 189 (key, description).

Spilographa Schiner, 1868 (in part), Reise der Novara, 2: 264–265 (*Spilographa* = *Zonosema* group).

Carpomyia, —Rondani, 1870, Boll. Soc. Ent. It., 99: 6.

Microrrhagoletis Rohdendorf, 1961, Ent. Obozr., 40: 187. [Monotypic; type (not examined): *Microrrhagoletis samojlovitshae* Rohdendorf, Bostandik District, southern Kazakhstan, USSR (LZI). NEW SYNONYMY.]

Megarrhagoletis Rohdendorf, 1961, Ent. Obozr., 40: 197. [Monotypic; paratype examined: *Megarrhagoletis magniterebra* Rohdendorf, southern Kazakhstan, USSR (LZI). NEW SYNONYMY].

Species not referable to Rhagoletis. Several species have been placed erroneously in *Rhagoletis* and the following list includes all the trivial names of these species as well as their accepted generic status at present.

caurina Doane = *Urophora formosa* (Coquillett)[6]
formosa Coquillett = *Urophora formosa* (Coquillett)
grindeliae Coquillett = *Urophora grindeliae* (Coquillett)
minuta Snow = *Procecidochares minuta* (Snow)
sapporensis Matsumura = *Matsumurania sapporensis* (Matsumura)

Generic diagnosis. Members of the genus *Rhagoletis* may be distinguished from other Trypetini by the presence of the following combination of characters: (1) ivory to yellowish white notopleural stripe reaching from humeral callus to the wing base; (2) wing pattern consisting of transverse yellow to brownish black bands; (3) r-m at center of 1st M_2; (4) frons slightly wider at vertex than at antenna but narrower than maximum width of eye; (5) gena about 0.12 to 0.23 height of head; (6) ocellar bristles approximately same length as upper fronto-orbitals; (7) three pairs of convergent lower fronto-orbitals, two pairs of reclinate divergent upper fronto-orbitals; (8) dorsocentrals located slightly before, on, or slightly behind line drawn between anterior supraalars, but always closer to anterior supraalars than to either transverse sulcus or acrostichals; (9) femora II and III without well developed spines along ventral margin; (10) male surstyli long and forcep-like, the prensisetae never apical or subapical.

Remarks. Zonosema, Microrrhagoletis, and Megarrhagoletis synonyms of Rhagoletis. This revision follows Hendel's 1927 treatment of the genus *Rhagoletis* in which

he regarded the predominantly Palearctic *Zonosema* Loew to be a synonym of *Rhagoletis* Loew. Collin (1947) considered these as distinct genera on the basis of wing coloration and habitus. However, when the wing patterns of *R. meigenii* (Loew), the type species of *Zonosema,* and the closely related *R. basiola* (Osten Sacken) and *R. alternata* (Fallen) are compared with *R. cerasi* (Linnaeus), the type species of *Rhagoletis,* it is obvious that the difference is only one of degree in infuscation (Stone, 1951). In considering *Rhagoletis* from North and South America, it also becomes apparent that habitus is no criterion for generic separation. *Zonosema* species resemble some of the Neotropical *Rhagoletis* more closely than they do their Eurasian congeneres. Therefore, based on the characters proposed by Collin, there is no reason to consider *Zonosema* distinct from *Rhagoletis.*

Benjamin (1934) and Rohdendorf (1961) also have recognized *Zonosema,* but their arguments for generic recognition based on body coloration, head shape, female genitalia, and spination on R_{4+5} are unwarranted. Complete intergradation of these characters between the two genera may be found in the New World *Rhagoletis.*

The light yellow body color regarded as typical of *Zonosema* occurs in both Nearctic and Neotropical *Rhagoletis* species which are closely related to entirely black forms (i.e., *R. juglandis–R. boycei* and *R. ferruginea–R. striatella*). In the case of setae on wing vein R_{4+5}, *Rhagoletis* from the Western Hemisphere may entirely lack setae on this vein (*pomonella* group) or may have only one or two at the junction of R_{2+3} and R_{4+5} (*cingulata* group, some members of the *suavis* group). In others, this vein is heavily setulose (some *suavis* group species, *R. striatella,* and most Neotropical species). Complete intergradation also occurs in the ratio of the length of the ovipositor and tergite VI, and no outstanding differences have been noted in the male genitalia.

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[6] See Foote, R. H., 1965, Family Tephritidae, p. 659, *in* Stone, A., et al. (eds.), A catalog of the Diptera of America north of Mexico. U.S. Dept. Agr. Handbook no. 276.

On biological grounds it would also seem unsound to recognize *Zonosema* as a distinct genus. Several species infest the same or closely related host fruits as certain members of the genus *Rhagoletis.*

The characters proposed by Rohdendorf to distinguish his monotypic genera *Microrrhagoletis* and *Megarrhagoletis* from *Rhagoletis* also do not appear sufficient for recognition at the generic level. He states that in body coloration both genera closely resemble *Rhagoletis* and that they are very much like *Zonosema* in head shape. Since *Zonosema* is a synonym of *Rhagoletis*, I can see no reason for retaining the two genera on the basis of these characters. Even the wing patterns of both genera are very similar to that of *R. cerasi* (Linnaeus). Furthermore, a host race (which may eventually prove to be a distinct species) of *R. cerasi* and the two new genera proposed by Rohdendorf infest the same host, *Berberis heteropoda* Schrenk.

Although Rohdendorf could find no differences between the male or female genitalia of *Microrrhagoletis* and *Rhagoletis*, he did consider the long ovipositor sheath of the female and long surstyli of the male in *Megarrhagoletis* of considerable taxonomic importance. The close similarity in all other characters, including host requirements, however, would indicate a rather close relationship. If generic status is to be based on characters such as the length of the ovipositor or ovipositor sheath without taking into consideration equally important characters, then a new genus should be created for *R. striatella* which has a short ovipositor sheath but an extremely long ovipositor. *R. striatella*, however, is closely related to species in South America which have much shorter ovipositors. For this reason, it is felt that the importance of this character has been given too much emphasis by Rohdendorf. Both genera should, therefore, be considered synonyms of *Rhagoletis.*

Status of Zonosemata, Carpomyia, and Rhagoletoides. The two genera most closely related to *Rhagoletis* are *Carpomyia* A. Costa and *Zonosemata* Benjamin. In the present revision these genera are recognized as distinct from *Rhagoletis,* but as more becomes known of the Neotropical and northeastern Asiatic species of all three genera it may be necessary to synonymize both *Rhagoletis* and *Zonosemata* with *Carpomyia.*

The minute size of the ocellar bristles in *Carpomyia* is the only character that effectively separates it from *Rhagoletis* whose ocellar bristles are of normal size. One Asiatic species of *Carpomyia, C. schineri* Loew, has the ocellars of normal length, and should therefore be placed in the genus *Rhagoletis.* Male and female genitalia as well as the host relationships of *Carpomyia* are very similar to *Rhagoletis* and offer no suitable characters for generic recognition.

The light yellow color of *Carpomyia* and the black pattern on the dorsum of the thorax have been used by some authors to separate *Carpomyia* and *Rhagoletis.* Color, as already pointed out in the case of *Zonosema*, is of questionable value as a criterion of generic distinction. The status of these two genera is therefore debatable and in need of careful consideration. A study of the chromosomes of *Carpomyia* may help to clarify the relationship somewhat as it has between *Zonosemata* and *Rhagoletis.*

The major differences between *Rhagoletis* and *Zonosemata* are in the position of the dorsocentral bristles, the number of lower fronto-orbital bristles, and their chromosome morphology. The surstyli of the male genitalia of *Zonosemata* are also considerably shortened beyond the prensisetae but in some ways resemble those of *R. striatella.*

In *Zonosemata* the dorsocentrals are located in line with the acrostichals, while in some *Rhagoletis*, such as *basiola* and *ferruginea*, the dorsocentrals may be inserted well behind the anterior supraalars but are always nearer to the anterior supraalars than to the acrostichals.

The number of lower fronto-orbital bristles is not always a reliable character

for separating *Zonosemata* and *Rhagoletis* because these bristles vary in number among species in both genera. *R. striatella* infesting the solanaceous genus *Physalis*, for instance, frequently has four pairs of lower fronto-orbital bristles, the number usually found in *Zonosemata*, while both *Z. electa* and *Z. vittigera* occasionally have only three pairs of lower fronto-orbitals.

In addition to the position of the dorsocentrals, the karyotypes also provide a means of distinguishing between the two genera. The chromosomes of *Rhagoletis* are of two basic types. Most of the species have five pairs of metakinetic chromosomes and a single pair of acrokinetic dots. Members of the *pomonella* group have three pairs of metakinetics, two pairs of acrokinetics, and a pair of dot chromosomes. With the exception of the dots, the chromosomes are long and distinct and their kinetichores are well defined. The sex chromosomes, when visible, are not heteropycnotic. Two species of *Zonosemata* studied cytologically, *Z. electa* (Say) and *Z. vittigera* (Coquillett) (Bush, 1965), have 12 chromosomes with extremely long heteromorphic and heteropycnotic sex chromosomes. The autosomes are metakinetic, minute, and have a fuzzy appearance. The sex chromosomes do not completely disappear during interphase, but remain as a diffuse heterochromatic mass in the nucleus. These differences probably represent a considerable degree of divergence and offer supporting evidence for maintaining *Zonosemata* as a distinct genus.

It should be noted, however, that the karyotype of *R. striatella*, with its long acrokinetic sex chromosomes and small metakinetic autosomes, is somewhat reminiscent of the *Zonosemata* karyotype. This observation, coupled with the facts that both described species of *Zonosemata* and *R. striatella* infest related plant genera and also show similarities in the number of lower fronto-orbital bristles, head shape, and certain characteristics of the male genitalia, indicates a possible distant relationship.

The distribution of three recently described species of *Zonosemata*, two from Mexico and one from Jamaica (Bush, 1965), suggests that this genus has its home base in either Central or South America. *Zonosemata* is, therefore, probably of Neotropical origin, and its true relationships with *Rhagoletis* may be more firmly established as more solanaceous infesting species are uncovered in Central and South America.

Recently (1960), a third monotypic genus, *Rhagoletoides* Foote, was described and is regarded as a close relative of *Rhagoletis*. The host of *Rhagoletoides latifrons* (van der Wulp) is unknown, but I have frequently encountered this species in Mexico on buffalo burr, *Solanum rostratum* Dunal, a solanaceous plant with a wide distribution in western North America and the central highlands of Mexico. In all probability, *R. latifrons* represents another relative of *Rhagoletis* and *Zonosemata* associated with the Solanaceae. *Rhagoletoides*, however, can easily be distinguished from *Rhagoletis* by the distinctive surstyli shape of the male genitalia and by the well developed apodeme on the genital ring. Both sexes of this genus also have well developed anterior and posterior ventral rows of spines on the mid and hind femora. These characters are lacking in *Rhagoletis*, *Carpomyia*, and *Zonosemata*.

Description. A detailed description of the generic characters is offered here and will not be repeated in the specific descriptions. *Head* (Figs. 1–3): 1.1–1.2 times wider than high; subquadrate in profile; light yellow to yellowish orange with postcranial region and mentum yellow or marked with light brown to black; ocellar triangle light brown to black; vertex narrower than maximum width of eye; eye about 1.25–1.55 times higher than wide; frons convex in profile, prominent at antennae, slightly wider at vertex than at antennae; antennae 0.61–0.73 length of face; third segment more than twice length of second; genae moderately narrow, from 0.12–0.24 height of head. Postcranial re-

gion slightly concave; face only slightly concave in profile; foveae deep, carina well developed; third antennal segment usually with a sharp awl-shaped tip, rounded in some Palearctic and Neotropical species; epistome slightly upturned; postgenae moderately bulging. Three pairs of convergent and slightly proclinate black fronto-orbitals, their bases in line with base of long black innervertical; two pairs black reclinate, divergent upper fronto-orbitals their bases in line with base of antennae; upper pair two-thirds length of lower; ocellars strongly proclinate, divergent, approximately same length as upper pair of upper fronto-orbitals; outerverticals black, about two-thirds innerverticals; postorbitals yellow to black, short, one-third to one-fourth length outervertical; zero to five intraverticals; postocellars yellow or black, about same length as upper pair of upper fronto-orbitals; zero to three yellow to black postverticals; yellow to black genal bristle always present, rarely weak; yellow gular present or weakly developed, sometimes undifferentiated from scattered yellow and black setae on postgenae and gulamentum; scattered setae also on lower two-thirds of frons and along lower half of ptinial sulcus; minute setae scattered over surface of eye; usually two to five black setae along dorsal margin of first antennal segment; second segment with well developed black pedicular setae, medial surface covered with short black decumbent setae, outer surface bare except for short setae along apical margin; arista black grading to yellow at base, normally pubescent. Face usually minutely pubescent, lighter in color than rest of head. *Thorax* (Figs. 5–6): base color highly variable, ranging from light yellow to black; notopleural stripe ivory to light yellow reaching from humeral callus along metapleuron to wing base; scutellum flat, trapezoidal. Dorsum covered with short decumbent thin setae and usually white to yellow pollinose microtrichia, the latter sometimes forming a distinct pattern of stripes. Normally two pairs scapulars with

supernumeraries occasionally present, arranged in tandem behind normal pair; position of dorso-centrals variable, ranging from slightly in front of line between anterior supraalars to almost midway between anterior supraalars and acrostichals; one to two, rarely three, mesopleurals; pteropleural sometimes minute. *Legs* (Figs. 7–9): coxa I with scattered microtrichia on anterior surface, and one to two black bristles on ventro-anterior margin; coxa II with five to seven black bristles and several short light brown setae on ventro-anterior margin; coxa III with black bristle and short light setae. Trochanter I bare; trochanter II with two short distinct black setae on dorso-apical margin; trochanter III with several short setae. Femur I with two to three ill-defined rows of bristles on dorsal surface, one to two rows of bristles on ventro-posterior surface; femur II with or without three to five somewhat poorly differentiated semierect setae on mid-anterior surface; femur III with three to eight bristle-like setae on apical end. Tibia II with long apical spur; tibia III with single row of short stout bristle-like setae on outer surface. *Wing* (Fig. 4): pattern consisting of yellow to black crossbands. R_1 setulose over entire length, node bare; R_{4+5} bare or with setae on dorsal surface; zero to four setae dorsally at junction of R_{4+5} and R_{2+3}, rarely setulose ventrally; two stout bristles at subcostal break. Anal cell variable, usually drawn out to point along $Cu_2 + 2nd$ A, occasionally blunt (Figs. 176–180); posterior crossvein at about mid-point of 1st M_2. First vein ends before mid-point of wing; fourth vein ends before apex of wing. *Abdomen* (Figs. 10–13): tergites II–IV in male, II–V or VI in female usually with white pollinose band along posterior margin, entirely absent or greatly reduced in some species. Tergites covered with fine setae approximately color of areas from which they arise; long black bristles along posterior and lateral margins of tergites III–V in male and III–VI in female. Sternites II–IV with well developed internal

apodemes. *Genitalia: male* (Fig. 14)—epandrium globose, covered with long bristles; surstyli usually long and forcep-like, short and broad in some species but prensisetae never terminal or subterminal. Ejaculatory apodeme variable, usually fan-shaped at apex; apical margin of fan occasionally thickened. Genital ring circular, without apodeme. *Female* (Figs. 15–16)—length of ovipositor sheath and ovipositor highly variable. Ovipositor with two or three minute preapical setae (Fig. 15). Two to three globular or cylindrical spermathecae always covered with scale-like papillae. Two accessory glands. Ventral receptacle resembling a cluster of grapes partially surrounding a central, more heavily sclerotized stem (Fig. 181).

Key to North American Species of RHAGOLETIS

The following key may be used to distinguish most of the North American species of *Rhagoletis*. In groups which have sibling species and present special problems in identification, reference must be made to the discussion of the species group concerned before a determination can be made.

1. Scutellum concolorous cream to yellowish white without distinct spot 2
   Scutellum with distinct cream to yellow circular or V-shaped scutellar spot 8

2. Wing pattern with small, triangular shaped intercalary band crossing cells R_1 and R_3 between medial and subapical crossbands (Fig. 212); body entirely yellow. Host: rose hips (*Rosa* spp.) .... *basiola* (Osten Sacken)
   Wing pattern without intercalary band; body yellow or black 3

3. Wing pattern without basal crossband (Fig. 195); body entirely yellow. Host: walnut (*Juglans* spp.) ....*juglandis* Cresson
   Wing pattern with basal crossband (i.e., Fig. 196); body yellow to black 4

4. Medial band normally not joined to subapical band (Figs. 192, 194, 196); if joined (Fig. 193), then body yellow to yellowish tan and postscutellum entirely dark brown or with dark brown horizontal srtipes 5
   Medial band broadly joined to subapical band (Figs. 191, 210); postscutellum entirely black or yellow, never brown or with vertical stripes 7

5. Veins R_{2+3} and R_{4+5} with horizontal fuscous markings between apical and subapical crossbands (Figs. 194, 196) 6
   Veins R_{2+3} and R_{4+5} without fuscous markings in this area; wing pattern as in Figure 192, rarely as in Figure 193. Host: walnut (*Juglans* spp.) .... *completa* Cresson

6. Thorax and abdomen black; wing pattern as in Figure 194. Host: walnut (*Juglans* spp.) .... *boycei* Cresson
   Thorax and abdomen predominantly tan to yellow; black markings limited to pleural and sternopleural areas; wing pattern as in Figure 196. Host: walnut (*Juglans* spp.) .... *zoqui* n. sp.

7. Body black, abdomen without white bands; wing pattern as in Figure 210. Host: sour and pin cherry (*Prunus* spp.) .... *fausta* (Osten Sacken)
   Body yellow to yellowish tan; wing pattern as in Figures 190–191. Host: walnut (*Juglans* spp.) .... *suavis* (Loew)

8. Scutellar spot V-shaped, wing pattern as in Figure 209. Host: husk tomato (*Physalis* spp.) ...... *striatella* van der Wulp
   Scutellar spot oval or trapezoidal shaped..... 9

9. Apical band of wing forming a fork (Fig. 204), or upper prong of fork separated from apical band by hyaline area (Fig. 203); surstyli with apical tuft of long setae (Figs. 79–82) .... *cingulata* group
   Apical band of wing entire; surstyli without apical tuft of setae 10

10. Basal crossband joined to medial crossband (i.e., Figs. 185 or 197) 11
    Basal crossband not joined to medial crossband 13

11. Medial band joined to apical and subapical bands to form an F-shaped pattern (Fig. 185) .... *pomonella* group
    Medial band not joined to either apical or subapical band 12

12. Male genitalia and aedeagus as in Figures 85, 101, 123; apex of phallothecae with tubular sac (Fig. 123S); female with two globular spermathecae (Fig. 162). Hosts: dogwood berries (*Cornus* spp.), blueberries (*Vaccinium* spp.) .... *tabellaria* (Fitch)
    Male genitalia and aedeagus as in Figures 86, 102, 124; apex of phallothecae bare; three cone-shaped spermathecae (Fig. 165). Host unknown ...... *persimilis* n. sp.

13. Apical band contiguous with costa over entire length (Fig. 202). Host: Oregon grape (*Mahonia* spp.) ...... *berberis* Curran
    Apical band separated from costa by hyaline area (i.e., Fig. 201) 14

14. Medial band joined to subapical band by

infuscated region in cell R₅ (Fig. 200).
Host unknown .... *ebbettsi* n. sp.
Medial band not joined to subapical
band 15

15. Usually with single mesopleural bristle;
anal cell not sharply pointed (Fig. 176);
posterior surface of head with black
horseshoe-shaped pattern; aedeagus with
setulose apical appendage (Fig. 127);
Two cylindrical spermathecae (Fig.
167). Host: currants and gooseberries
(*Ribes* spp.) .... *ribicola* Doane
Usually two to three mesopleural bristles;
anal cell sharply pointed (Fig. 178);
black band only across upper third of
head, lower two-thirds yellow; aedeagus
without apical appendage (Fig. 125);
two globular spermathecae (Fig. 163).
Host: juniper berries (*Juniperus* spp.)
.... *juniperina* Marcovitch

POMONELLA SPECIES GROUP

The outstanding feature of this group is
the close morphological similarity between
the various species in contrast to their dis-
tinct host requirements. *R. pomonella,* the
apple maggot, is probably the best known
member of the group and is also one of
the most economically important species
of *Rhagoletis* in North America. In 1867
Benjamin Walsh described *Trypeta pomo-
nella* from specimens reared from haws in
Illinois and apples in Long Island, New
York. This description followed shortly
after the realization that *pomonella* was
becoming a serious pest of apples in north-
eastern United States, particularly in the
Hudson River Valley. It is from this re-
gion that the apple infesting population is
thought to have spread over eastern United
States and Canada (see Illingworth, 1912,
and O'Kane, 1914, for summary). Since
that time, *pomonella*-like *Rhagoletis* have
been reared from blueberries, huckleberries,
dogwood berries, snowberries, and several
other fruits.

There has been controversy over the
status of these forms with such authors as
Brues (1924), Cresson (1929), Thorpe
(1930), and Pickett (1937) considering
them as simply host races or, at most, sym-
patric subspecies. Others such as Curran
(1932), Benjamin (1934), Hall (1938), and

Christenson and Foote (1960) have re-
garded all or some of the forms as distinct
species.

The results of the present investigation
show that, in the broad sense, *R. pomonella*
actually includes at least four species and
possibly more. Morphological differences
are slight, and for this reason I have relied
heavily on biological criteria for clues to
the status of these "cryptomorphic" species.

The decision to recognize the four species
now included in the *pomonella* group is
based on the following observations.

(1) Crosses and forced oviposition experi-
ments attempted by independent workers
(Lathrop and Nickels, 1932; McAlister and
Anderson, 1935; Pickett, 1937; Hall, 1938,
1943; Pickett and Neary, 1940) indicate
that reproductive isolation between the
most closely related sympatric species, *R.
pomonella, mendax,* and *cornivora,* is es-
sentially complete. The results of these
experiments are summarized in Table 2.
In the case of crosses attempted between
pomonella and *mendax,* viable F₁ progeny
were produced only between *pomonella*
females × *mendax* males, but not in the
reciprocal cross.

(2) There are slight but consistent mor-
phological differences between sympatric
populations of the three eastern species
which could not be maintained if gene
flow existed between them. An example of
these differences may be seen in the Dice-
Leraas diagrams of Figure 21, illustrating
the difference in ovipositor length. It
should be noted that there is no overlap
in ovipositor length between northeastern
pomonella and the sympatric populations
of *mendax* and *cornivora.* The difference
in ovipositor length between *mendax* and
cornivora, although not as dramatic, is also
interesting, and considering the small vari-
ability in related species, the difference is
probably significant. These differences will
be discussed more fully in the taxonomic
treatment of each species.

(3) Differences in behavior and ecology
have been demonstrated in *pomonella* and

TABLE 2.   RESULTS OF CROSSES BETWEEN "HOST RACES" OF *Rhagoletis* IN THE *pomonella* SPECIES GROUP. COMPILED FROM 1) PICKETT (1937), PICKETT AND NEARY (1940); 2) HALL (1938, 1943); 3) McALISTER AND ANDERSON (1935); 4) LATHROP AND NICKELS (1932).

Host of ♂	Host of ♀	Oviposited on	Pupae recovered	Author(s)
apple	apple	apple or haw	+	1, 2
apple	apple	blueberry	+	1, 4
haw	haw	apple or haw	+	1, 2
haw	apple	apple or haw	+	1
apple	haw	apple or haw	+	1
blueberry	blueberry	blueberry	+	1, 3
blueberry	apple	apple or blueberry	+	1, 3
apple	blueberry	apple	−	1, 3
apple	blueberry	blueberry	−	1, 3
haw	blueberry	haw or blueberry	−	1
blueberry	haw	haw or blueberry	−	1
Cornus	*Cornus*	*Cornus*	+	2
Cornus	*Cornus*	apple or haw	−	2
Cornus	apple or haw	no mating	−	2
apple or haw	*Cornus*	no mating	−	2
apple or haw	apple or haw	*Cornus*	+	2

mendax, and are illustrated in the following examples.

Females of *mendax* are known to have great difficulty ovipositing in apples or haws (Lathrop and Nickels, 1932; Pickett, 1937). On the other hand, *pomonella* from apples will readily oviposit in blueberries in the laboratory, but a larva usually needs more than one blueberry to complete development (Lathrop and Nickels, 1932), a difficult hurdle to overcome in the field except perhaps under exceptional conditions (McAlister, 1932). Also, when second instar *mendax* larvae are transferred from blueberries to haws or apples (first instar larvae die), the resulting pupae and adults are of normal size for *mendax* (Lathrop and Nickels, 1932). This indicates that, in the case of *mendax*, size for the most part is probably determined by the genotype of the species and not by nutrition.

Another outstanding difference between these two species is the method of egg deposition. *R. mendax* places the egg directly beneath the skin of the berry, while *pomonella* inserts the egg well into the flesh of the fruit, usually to a depth equivalent to the full length of the ovipositor (Lathrop and Nickels, 1932).

The biology of *cornivora* has not been studied in any detail. However, *pomonella* has been induced to oviposit in dogwood berries under laboratory conditions and the resulting adults were smaller than normal. *R. cornivora*, which normally oviposits in dogwood berries, refused to oviposit in apples. This indicates that these two species have quite different host preferences.

Diagnosis. Members of the *pomonella* group form a well delineated complex of species distinguished from all other species groups in the genus by their distinctive karyotype, wing pattern, and bicolored halteres. Unlike the five pairs of metakinetic and a single pair of acrokinetic dot chromosomes found in most other groups, all species in the *pomonella* group have only three metakinetic chromosomes plus two rod-shaped acrokinetic chromosomes and a pair of acrokinetic dot chromosomes. In the wing pattern, both the apical and subapical wing bands are joined to the medial band along the anterior margin of the wing; the medial band is broadly joined to the basal band along the posterior margin of the wing (Figs. 185–189). The halteres are bicolored with the upper half black and the lower half yellow. In all

other *Rhagoletis* these structures are concolorous yellow to tan.

Description. Because of the slight morphological differences between species of the *pomonella* group, a detailed description of the whole group is presented, followed by a discussion and diagnosis of each species. Body and wing measurements are presented in Tables 3A–3B. *Head* (Figs. 22–26): a black horizontal stripe across postcranium; upper third of occiput and upper half of frontalia yellowish brown; lower half of frons and genae usually lighter golden yellow; parafrontalia, anterior region of postgenae, postorbital regions, and face light creamish yellow; antennae yellowish orange; mentum black. Postocellar, genal, and poorly developed gular bristles yellow; all other major bristles black; setae on postgenal region and gulamentum mostly yellow, with setae on genae and along basal margin of ptinial sulcus black; usually only one postvertical with 7 to 15 postorbitals. *Thorax* (Fig. 45): black except for cream colored notopleural stripe and circular scutellar spot. Dorsum covered with black and white short decumbent setae and white pollinose microtrichia arranged in four rows; outer row reaching from scapulars posteriorly to a point in line with base of prescutellars; medial row reaching only to a point midway between dorsocentrals and prescutellars; medial rows separated by a wide black band; two pairs yellow scapulars; dorsocentrals in line with anterior supraalars; two mesopleurals, lower usually shorter than upper. Postscutellum shining black; halteres with upper half black, lower half yellow. *Legs*: coxa I yellow on anterior surface, black on posterior surface; coxae II and III black. Femur I variable in color with anterior surface always light yellow to yellowish orange, posterior surface yellow or heavily marked with black; femora II and III dark brown to black except for yellow to yellowish orange knees. All tibiae yellow to yellowish orange; tibia III sometimes with brown or black shading particularly near base. Tarsal segments

entirely yellow to yellowish orange. *Wing* (Figs. 185–189): in transmitted light basal band joined broadly to medial band along Cu_2 + 2nd A. Medial band joined to apical band in cell R_1 and R_3, and to subapical band in cells R_5 and part of cell 1st M_2; hyaline area between apical band and costa narrow at junction of R_1 and costa, but broadening posteriorly. Anterior margin of apical band smooth (Fig. 188) or broken in step-like fashion (Fig. 186). Width of subapical band variable with species. R_{4+5} bare over entire length and at junction with R_{2+3}. Anal cell pointed. *Abdomen* (Figs. 47–48): all segments black; tergites II–IV in male (Fig. 47) and II-V in female (Fig. 48) with white pollinose band along posterior margin. Band on tergite V in female sometimes reduced or, rarely, entirely absent. *Genitalia:* male—epandrium black; surstyli golden yellow, variable in shape depending on species. Aedeagus (Figs. 113–116) with long recurved finger-like apical appendage covered with long setae; vesica usually bifurcate. Ejaculatory apodeme normal (Figs. 135–138). *Female—* variation in ovipositor length shown in Figure 21; two minute preapical setae on ovipositor; ovipositor sheath brown to shining black. Three cylindrical spermathecae covered with long scale-like papillae (Fig. 156), two (one usually shorter than the other) on right side of abdomen, a single spermatheca on left side; apical third of spermathecae usually bare.

Rhagoletis pomonella (Walsh)

Trypeta pomonella Walsh, 1867, Amer. J. Hort., 2: 338–343. [Syntypes examined: lectotype ♀, by present designation, Ill. (Loew Coll.) (MCZ, Syntype No. 25702); ♀, no locality (Osten Sacken Coll.) (MCZ, No. 25702).]

Trypeta (Rhagoletis) pomonella, —Loew, 1873, Smithson. Misc. Coll., 256: 265–268 (description).

Rhagoletis pomonella, —Snow, 1894, Kansas Univ. Quart., 2: 164, pl. 6, fig. 3 (description). —Doane, 1898, Ent. News, 9: 69 (syn. *R. zephyria* Snow). —Aldrich, 1909, Canad. Ent., 41: 72, pl. 4, fig. 4 (in key, discussion). — Bezzi, 1911, Boll. Lab. Zool. Portici, 5: 7, 15–16, 18–19. —Curran, 1924, Rept. Ent.

Soc. Ontario, 54: 56–57 (taxonomy of host races). —Cresson, 1929, Trans. Amer. Ent. Soc., 55: 409–410, pl. 16, fig. 7 (taxonomy). —Curran, 1932, Amer. Mus. Nov., 526: 6–8, fig. 2 (taxonomy). —Benjamin, 1934, U.S. Dept. Agr. Tech. Bull., 401: 9, 12, fig. 13 (taxonomy, in Florida). —Pickett, 1937, Canad. J. Res. (D), 15: 54–60 (crossbreeding host races, male genitalia). —Phillips, 1946, Mem. Amer. Ent. Soc., 12: 61, 64, 66, 67, 69–72, figs. 28, 73, 133, 134, 175 (larval morphology, in key).

R. pomonella usually infests only fruits of the subfamily Pomoideae (Rosaceae), which includes several closely related genera (see *Hosts*). The single exception to this essentially oligophagous habit is a "host race" associated with wild and cultivated plums (*Prunus* spp., subfamily Prunoideae). This population may already have reached the species level, but further study is necessary to establish its status with certainty.

Benjamin (1934) noted that Florida specimens reared from wild plums were much smaller than those reared from haws; but he found that adults which emerged from pupae sifted from soil beneath infested plum trees closely approximated the size of specimens reared from *Crataegus*. He attributed this size difference to a deterioration in the nutritive qualities of plums after they had been picked.

In examining the specimens used by Benjamin in his revision, I have also found a distinct difference in body size and ovipositor length between the plum and haw populations (Fig. 21; Tables 3A–3B). However, I was unable to locate enough specimens that had emerged from pupae collected under infested plum trees to confirm Benjamin's observation that the method of rearing may influence body size.

In the absence of sufficient biological and distributional information, it is impossible to satisfactorily evaluate these slight differences and resolve the status of the plum and haw forms. Therefore, the two populations will be considered conspecific in this revision.

It should also be noted that there is an indication that the apple and haw forms may be diverging rapidly. A significant difference in ovipositor length between the two populations collected within 15 miles of each other in Nova Scotia suggests that they are already fairly restricted to their respective hosts (Fig. 21). These flies were captured on the host plant to eliminate any effects of rearing technique. Furthermore, the similarity in ovipositor length between *pomonella* on apples in widely separated areas and a correspondingly large variation in this structure between allopatric haw populations supports the conclusion reached by past workers that the apple infesting form originated from a single population in eastern United States and spread to other localities. Again, the lack of information makes it necessary to consider these two populations conspecific.

It is uncertain whether the *pomonella*-like flies reared from other genera of Pomoideae are conspecific or represent distinct host races or species. Nicholson (1929–30) noted the small size of three specimens reared from *Aronia arbutifolia* (L.) L. f. in Florida. The *pomonella* specimens I have examined reared from *Cotoneaster* (*Pyracantha*) sp. from Beaumont, Texas, are also very small, averaging smaller than *mendax* and *zephyria*. *Cotoneaster*, like the apple, is an introduced plant and cannot be considered a native host. These host populations warrant careful investigation as they offer an opportunity to study the process of speciation of phytophagous insects under natural conditions.

Diagnosis. The northeastern and Mexican populations of *pomonella* infesting *Crataegus*, *Pyrus*, *Prunus* (plums), and possibly *Aronia* and *Amelanchier*[7] can be distinguished from *cornivora*, *mendax*, and *zephyria* by ovipositor length (Fig. 21), shape and proportions of the surstyli (Table 4; Figs. 71, 90), large body size (Tables

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[7] Adults have not been reared from *Amelanchier*. For discussion of material reared from *Aronia* see *Hosts*.

	R. pomonella Nova Scotia	R. [illegible] Fla.	[illegible]	R. pomonella [illegible]	R. [illegible] NE	R. mendax Fla.	R. zephyria	R. [illegible]
n	10	5	[illegible]	10	10	10	10	7
[illegible]	1.00±.017 (.91-1.08)	[illegible]	[illegible] (.51-.73)	.91±.025 (.78-1.03)	.76±.013 (.66-.82)	.79±.012 (.72-.87)	.78±.021 (.65-.85)	.81 (.73-.91)
[illegible]	1.54±.023 (1.20-1.63)	1.50 [illegible]	1.04 [illegible]	1.53±.030 (1.35-1.65)	1.24±.027 (1.11-1.33)	1.27±.020 (1.12-1.36)	1.25±.037 (1.00-1.38)	1.38 (1.26-1.52)
[illegible]	[illegible]±.014 (1.22-1.3[illegible])	[illegible]	[illegible] [illegible]	1.2[illegible]±.030 (1.13-1.40)	1.03±.028 (.85-1.16)	1.09±.012 (1.00-1.15)	1.07±.035 (.95-1.17)	1.16 (1.08-1.24)
[illegible]	.78±.011 [illegible]	.77 [illegible]	.75 [illegible]	.81±.01[illegible] (.68-.86)	.62±.013 (.56-.67)	.65±.012 (.56-.71)	.62±.01[illegible] (.53-.67)	.66 (.62-[illegible])
[illegible]	1.02±.015 [illegible]	[illegible] [illegible]	.76 [illegible]	1.04±.025 (.92-1.14)	.85±.020 (.75-.93)	.8[illegible]±.014 (.79-.95)	.8[illegible]±.026 (.7[illegible]-.97)	.94 (.88-[illegible])
[illegible]	.55±.004 [illegible]	.4[illegible] [illegible]	.40 [illegible]	.46±.012 [illegible]	.42±.010 (.37-.49)	.41±.00[illegible] (.35-.44)	.45±.01[illegible] (.35-.51)	.51 (.4[illegible]-.57)
[illegible]	.5[illegible]±.00[illegible] [illegible]	.51 (.4[illegible]-.54)	[illegible]	.54±.010 (.4[illegible]-.57)	[illegible] (.37-.51)	.45±.007 (.41-.49)	.45±.014 (.[illegible]7-.51)	.47 (.42-.51)
[illegible]	[illegible] (.7[illegible]-.83)	.7[illegible] [illegible]	.7[illegible] (.47-.77)	.75±.021 [illegible]	.6[illegible]±.01[illegible] (.51-.67)	.61±.013 (.53-[illegible])	[illegible]±.020 (.48-.[illegible]7)	[illegible] (.65-.77)
[illegible]	[illegible] (.22-.2[illegible])	.22 (.1[illegible]-.24)	.17 [illegible]	.2[illegible]±.0[illegible] (.16-.24)	.18±.004 (.1[illegible]-.20)	.17±.002 (.14-.20)	.20±.0[illegible] (.15-.22)	.2[illegible] (.20-.27)
[illegible]	[illegible]4±.02[illegible] ([illegible]-2.14)	[illegible]	1.2[illegible] [illegible]	[illegible]±.04[illegible] [illegible]	1.53±.0[illegible] (1.37-1.7[illegible])	1.50±.023 (1.42-1.7[illegible])	[illegible] (1.24-1.75)	1.70 (1.50-1.91)
n	[illegible]	1[illegible]	[illegible]	[illegible]	[illegible]	10	10	[illegible]
[illegible]	[illegible]4±.045 (2.[illegible])	[illegible]±.024 [illegible]	[illegible] (1.4[illegible]-2.70)	[illegible]±.054 [illegible]	2.60±.026 (2.26-2.72)	2.4[illegible]±.045 (2.20-2.71)	[illegible] (2.[illegible]-3.17)	2.60 (2.50-2.66)
W.W.	[illegible]±.022 (1.[illegible]4-2.0[illegible])	1.72±.02 [illegible]	1.2[illegible] (1.11-1.4[illegible])	1.82±.0[illegible] (1.67-2.16)	1.47±.043 (1.28-1.[illegible]7)	1.39±.025 (1.23-1.50)	1.64±.0[illegible] (1.[illegible]-1.79)	1.54 (1.42-1.67)

Table [illegible]A. Body and wing measurements of males of the pomonella species group. Figures represent mean, standard error, and range.

	[illegible] Nova Scotia	[illegible] Fla.	[illegible] Texas	R. [illegible] Mexico	R. [illegible] NE	R. [illegible] Fla.	R. [illegible]	R. [illegible]
n	[illegible]	[illegible]	[illegible]	1[illegible]	1[illegible]	1[illegible]	[illegible]	[illegible]
[illegible]	[illegible] ([illegible]-1.14)	.[illegible]±.01[illegible] (.[illegible]2-1.05)	.70 (.5[illegible]-.77)	1.01±.025 (.90-1.16)	.78±.014 (.68-.84)	.78±.018 (.68-.85)	[illegible]±.015 (.77-.90)	.87 (.70-1.04)
[illegible]	[illegible] (1.54-1.73)	1.64±.02 (1.54-1.75)	1.24 (1.12-1.50)	1.67±.036 (1.53-1.8[illegible])	1.26±.026 (1.13-1.40)	1.28±.035 (1.03-1.43)	1.30±.026 (1.21-1.44)	1.35 (1.18-1.53)
H.I	[illegible] (1.30-1.52)	1.3[illegible]±.01[illegible] (1.27-1.43)	1.01 (.91-1.1[illegible])	1.34±.013 (1.12-1.57)	1.06±.028 (.90-1.20)	1.06±.025 (.94-1.20)	1.12±.02[illegible] [illegible]	1.18 (1.02-1.2[illegible])
[illegible]	.80±.013 (.74-.86)	[illegible] (.74-.83)	.61 (.55-.71)	.82±.013 (.74-.88)	.61±.011 (.53-.65)	.66±.01[illegible] (.55-.73)	.64±.017 (.56-.70)	.65 (.56-.70)
[illegible]	1.14±.020 (1.05-1.22)	1.14±.017 (1.05-1.19)	.83 (.75-.97)	1.11±.026 (1.00-1.23)	.88±.022 (.76-.98)	.91±.026 (.75-1.03)	.90±.021 (.82-1.02)	.95 (.81-1.07)
[illegible]	.5[illegible]±.014 (.52-.[illegible]5)	.55±.00[illegible] (.52-.[illegible]0)	.39 (.35-.47)	.53±.023 (.44-.66)	.43±.012 (.38-.49)	.43±.011 (.35-.49)	.47±.00[illegible] (.43-.52)	.48 (.41-.55)
[illegible]	.57±.012 (.52-.[illegible]4)	.5[illegible]±.00[illegible] (.50-.60)	.43 (.41-.43)	.60±.015 (.53-.68)	.46±.011 (.41-.52)	.46±.00[illegible] (.41-.50)	.46±.010 (.40-.51)	.46 (.41-.50)
[illegible]	.[illegible]2±.017 (.74-.8[illegible])	[illegible]±.013 (.75-.[illegible]3)	.[illegible]1 (.5[illegible]-.73)	.[illegible]4±.020 (.74-.[illegible]0)	.61±.018 (.50-.68)	.62±.017 (.52-.70)	.65±.015 (.55-.72)	.69 (.53-.80)
[illegible]	[illegible] (.23-.3[illegible])	.2[illegible]±.005 (.22-.2[illegible])	.17 (.14-.20)	.2[illegible]±.020 (.24-.36)	.18±.006 (.16-.20)	.18±.006 (.15-.21)	.21±.005 (.17-.22)	.23 (.20-.26)
[illegible]	2.[illegible]0±.047 (1.[illegible]3-2.50)	2.1[illegible]±.0[illegible]4 (1.[illegible]4-2.1[illegible])	1.62 (1.42-2.00)	2.24±.061 (1.88-2.58)	1.68±.035 (1.45-1.86)	1.64±.033 (1.40-1.76)	1.65±.053 (1.42-1.91)	1.81 (1.60-2.10)
n	24	10	[illegible]	1[illegible]	24	10	[illegible]	[illegible]
[illegible]	4.10±.054 (3.[illegible]4-4.43)	[illegible]7±.05[illegible] (4.0[illegible]-[illegible].41)	2.60 (2.5[illegible]-3.18)	3.83±.094 (3.21-4.75)	3.01±.057 (2.36-3.44)	2.78±.021 (2.35-3.02)	3.22±.050 (2.76-3.53)	3.21 (3.01-3.56)
[illegible]	2.25±.027 (1.97-2.43)	2.07±.0[illegible] (1.[illegible]0-2.[illegible])	1.52 (1.3[illegible]-1.73)	2.17±.051 (1.80-2.5[illegible])	1.72±.033 (1.38-1.97)	1.59±.030 (1.52-1.71)	1.88±.032 (1.62-2.15)	1.85 (1.66-2.15)

Table [illegible]B. Body and wing measurements of females of the pomonella species group. Figures represent mean, standard error, and range.

TABLE 4. SURSTYLI RATIO AND ANGLE OF THE *pomonella* SPECIES GROUP. FOR METHOD USED IN MAKING MEASUREMENTS SEE FIGURE 239. FIGURES REPRESENT MEAN, STANDARD ERROR AND RANGE.

SPECIES	LOCALITY	n	RATIO	ANGLE A
pomonella	all pop.	21	.81 ± .014 (.68–.92)	143 ± 1.15 (134–153)
mendax	NE	10	.87 ± .019 (.75–.93)	139 ± 0.34 (135–146)
mendax	Fla.	6	.85 (.69–1.00)	146 (139–151)
zephyria	all pop.	16	.67 ± .020 (.50–.84)	160 ± 1.32 (153–169)
cornivora	NE	3	1.00 (.98–1.01)	139 (138–141)
cornivora	Fla.	3	.79 (.77–.82)	145 (142–157)

TABLE 5. MEDIAL AND SUBAPICAL CROSSBAND WIDTH RATIOS OF THE WING FOR THE *pomonella* SPECIES GROUP. FIGURES INCLUDE BOTH MALES AND FEMALES AS NO DIFFERENCE BETWEEN THE SEXES WAS NOTED. FOR METHOD OF MAKING MEASUREMENTS SEE FIGURE 238.

SPECIES	LOCALITY	n	RATIO
pomonella	NE	48	.43 ± .008 (.30–.56)
pomonella	Mex.	40	.39 ± .008 (.30–.48)
pomonella	Fla.	20	.43 ± .012 (.30–.53)
mendax	NE	40	.59 ± .008 (.51–.69)
mendax	Fla.	23	.47 ± .012 (.34–.60)
cornivora	NE	10	.53 ± .015 (.46–.60)
cornivora	Fla.	11	.48 ± .011 (.43–.55)
zephyria	NW	38	.54 ± .014 (.41–.72)

3A–3B), and ratio between the width of the medial and subapical crossbands (Table 5). Finally, the presence of heavy black shading on the posterior surface of femur I in *pomonella* offers a useful morphological character in differentiating between this species and the sympatric *mendax* and *cornivora*.

In Florida the females of *pomonella* cannot be distinguished readily from *cornivora* or *mendax* except on the basis of body size (Table 3B, i.e., thorax length). Ovipositor length and color pattern show considerable overlap in this region. Males may be distinguished on the basis of surstyli ratio (Table 4) and overall size (Table 3A). For biological reasons already outlined, the Florida representatives of these three species must be considered distinct even though preserved material cannot always be identified without suitable host data.

Geographical variation. Three trends in geographical variation are evident in *pomonella*. The most conspicuous is the pronounced reduction in size in the extreme southern limits of its range in eastern North America and Texas where xeromesophytic conditions prevail (for example, see Fig. 21; Tables 3A and 3B). *R. pomo-*

nella infesting haws and plums in Florida and *Cotoneaster* sp. in Texas may be no larger in certain body measurements than specimens of *mendax* or *cornivora* from Massachusetts. This trend is reversed in the Mexican population of *pomonella* which is only slightly smaller than the northeastern representative of this species.

The difference in size between the northeastern and southern populations of *pomonella* is sharp enough so that an ill-defined geographic division can be drawn between them, represented by a broad area in southern South Carolina and northern Georgia. This region is proposed only as a probable area of transition between the smaller sized Florida *pomonella* population and the larger sized northeastern populations. I have been able to examine only a few specimens of *pomonella* from these two states and they have not provided enough information to establish just where the shift may occur or if the two populations

are actually completely isolated from one another.

A second trend is toward a slight reduction in the intensity and distribution of black coloring in the most southern populations, although this is not as marked as a similar shift of color pattern noted in *R. cingulata*.

A third trend is apparent between Mexican and northeastern populations in the wing pattern. In specimens from Mexico there is usually a hyaline spot at the base of the apical band just apicad of its junction with the medial band (Fig. 186). This spot was never found in the northeastern specimens examined, although this region may be somewhat lighter than the rest of the band in teneral individuals.

Chromosome number and morphology (Figs. 213–214). The diploid number is 12; the MCA number is 18 as there are three pairs of metakinetic chromosomes, two rod-shaped acrokinetic chromosomes, and a single pair of acrokinetic dot chromosomes. No morphologically differentiated heterochromosomes (XY) were observed. A secondary constriction is usually present at metaphase in one arm of the shortest metakinetic chromosome.

Source of cytological material: *Crataegus* spp., Cambridge, Mass., Sept. 20, 1962; Mil Cumbres, Michoacan, Mexico, Sept. 9, 1961. *Pyrus Malus*, Kentville, Nova Scotia, Oct. 26, 1962; West Crampton, New Hampshire, Aug. 27, 1960; Zaqualtipan, Hidalgo, Mexico, Aug. 15, 1957.

Courtship behavior. I was unable to get this species or any other member of the *pomonella* group to perform normally in the laboratory, and I have not observed courtship in the field. Males may be seen patrolling apples and haws, and mated pairs are frequently seen on foliage near fruit.

Parasites. The following hymenopterous parasites have been recorded from *pomonella: Opius lectus* Gahan, *O. alloeus* Muesebeck (=*ferrugineus* of authors), *O. melleus* Gahan, *Aphaereta muscae* Ashmead (Bra-

conidae); *Galesus* sp. (Diapriidae); Eulophidae (specimen damaged, genus and species unknown); *Pattasson conotracheli* (Girault) (=*Anaphoidea* of authors). For further details, see Porter and Alden (1921), Middlekauff (1941), and Muesebeck (1956).

Hosts. The recorded hosts of *pomonella* are summarized in Table 6. Although *pomonella* has been found to infest several genera of the family Rosaceae, it may still be considered essentially oligophagous. With the exception of the population on plums, which may yet prove to be a distinct species (see introductory remarks), it is associated only with members of the subfamily Pomoideae. This group includes several closely related genera[8] considered by some botanists to represent a single genus (Sax, 1931, 1933; Lawrence, 1951). Intergeneric graft hybrids and crosses have been made between many genera in this subfamily indicating a close relationship (see Weber, 1963, for summary).

The major hosts of *pomonella* in the Pomoideae are hawthorn (*Crataegus*) and apples (*Pyrus*), but not all varieties and species of these plants serve as hosts in the field or under laboratory conditions (Wellhouse, 1922; Porter, 1928; Pickett, 1937).

The association of *pomonella* with apples in both northeastern United States and Mexico is a recent one with the first recorded infestation published by Ward in 1866 (vide Illingworth, 1912), over 200 years after the introduction of the apple into New England from Europe. It is very likely that *pomonella* was infesting apples for several years before 1866 as Walsh (1867) reported infestations in this fruit from widely separated areas in the Hudson River Valley. It is not known when *pomonella* became established on apples in Mexico, but the first apple trees were planted in 1522 (Bustamente; vide Stand-

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[8] *Pyrus* (including *Malus*), *Crataegus*, *Sorbus*, *Aronia*, *Amelanchier*, *Cotoneaster*, and others

ley, 1922), about 100 years before their introduction into New England. The shift from a native host to apples probably occurred independently in these two areas as both populations on apples have maintained the distinct wing pattern of the parent *Crataegus* population.

The question of the original native host of the apple population has never been adequately answered. The most logical suspect in eastern United States would be the native wild crabapples. However, native crabs have never been found infested with *pomonella* (O'Kane, 1914; Porter, 1928), but introduced Siberian crabs such as *Pyrus baccata* L. and *baccata* × *Malus* hybrids are readily attacked (Ross, 1913; O'Kane, 1914). The reason for this preference has not been studied, but it has been suggested that the fruit of most North American species ripens too late for *pomonella* to complete its development before winter sets in (O'Kane, 1914). Apparently there is also a considerable difference between Siberian and North American crabs as attempts to hybridize the two have never been successful (Wood, personal communication). On the other hand, native crabs and apples do hybridize (McVaugh, 1943), but it is not known if these hybrids become infested with *pomonella*.

The absence of native crabs in Mexico and the presence of infested *Crataegus*, coupled with the observation that native crabs are not attacked in northeastern United States, indicate that the shift occurred from *Crataegus* to apples in both regions. *Crataegus*, therefore, is the most likely original native host of the apple population.

The single exception to the host specificity of *pomonella* for members of the Pomoideae is the "host race" on wild and cultivated plums (*Prunus*, subfam. Prunoideae). The distribution of *pomonella* in relation to this host is not well known. The reported infestations from Florida (Benjamin, 1934) and New York (Greene, 1927), as well as an examination of a series of

specimens reared from plums in New Brunswick, Canada, indicate that this race is distributed over most of the range of the native plum species.

The peach, *Prunus persica* (L.) Batsch, has also been recorded as an occasional host of *pomonella* (Porter, 1928), but apparently infestations are rare, have never reached economic proportions, and occur only when peaches are growing near infested apples. This introduced plant therefore cannot be regarded as a normal host for *pomonella*.

Distribution (Map 1). *R. pomonella* is limited to areas east of the 100th meridian along the transitional zone, except for an occasional introduction into apple growing regions of the West. It reaches north only to the most southern part of the eastern Canadian provinces and south to eastern Texas and northern Florida. This species is also found in the central highlands of Mexico but the exact limits of its distribution in this country are unknown.

Map 1 shows the distribution of the two major native host genera, *Crataegus* and *Prunus*. All the known species of both genera are lumped to show the known distribution of *pomonella* in relation to the potential host species.

It should be mentioned that *pomonella* may have a much wider distribution than present records indicate. In addition to the specimens I have reared from *Crataegus* and *Pyrus Malus* in Mexico, infested fruits of both genera have been intercepted from Mexico and Costa Rica (Benjamin, 1934; U. S. Dept. Agr. unpublished interception records). Apples are not grown commercially in Costa Rica, but *Crataegus*, although not native, grows as an escape at high elevations (Standley and Steyermark, 1946). *R. pomonella*-like larvae have also been found in apples growing in Colombia (Garcés and Gallego, 1947), but the extent of the infestation and accurate identification of the species involved have not been determined. *Crataegus* is not native to South America. It was introduced by In-

MAP 1

- ●   RHAGOLETIS POMONELLA
- ○   LOCALITY CITED IN LITERATURE
- ——   CRATAEGUS SPP. (POMOIDEAE)
- ··········   PRUNUS SPP. (PLUM: PRUNOIDEAE)

SCALE

LAMBERT'S AZIMUTHAL EQUAL AREA PROJECTION
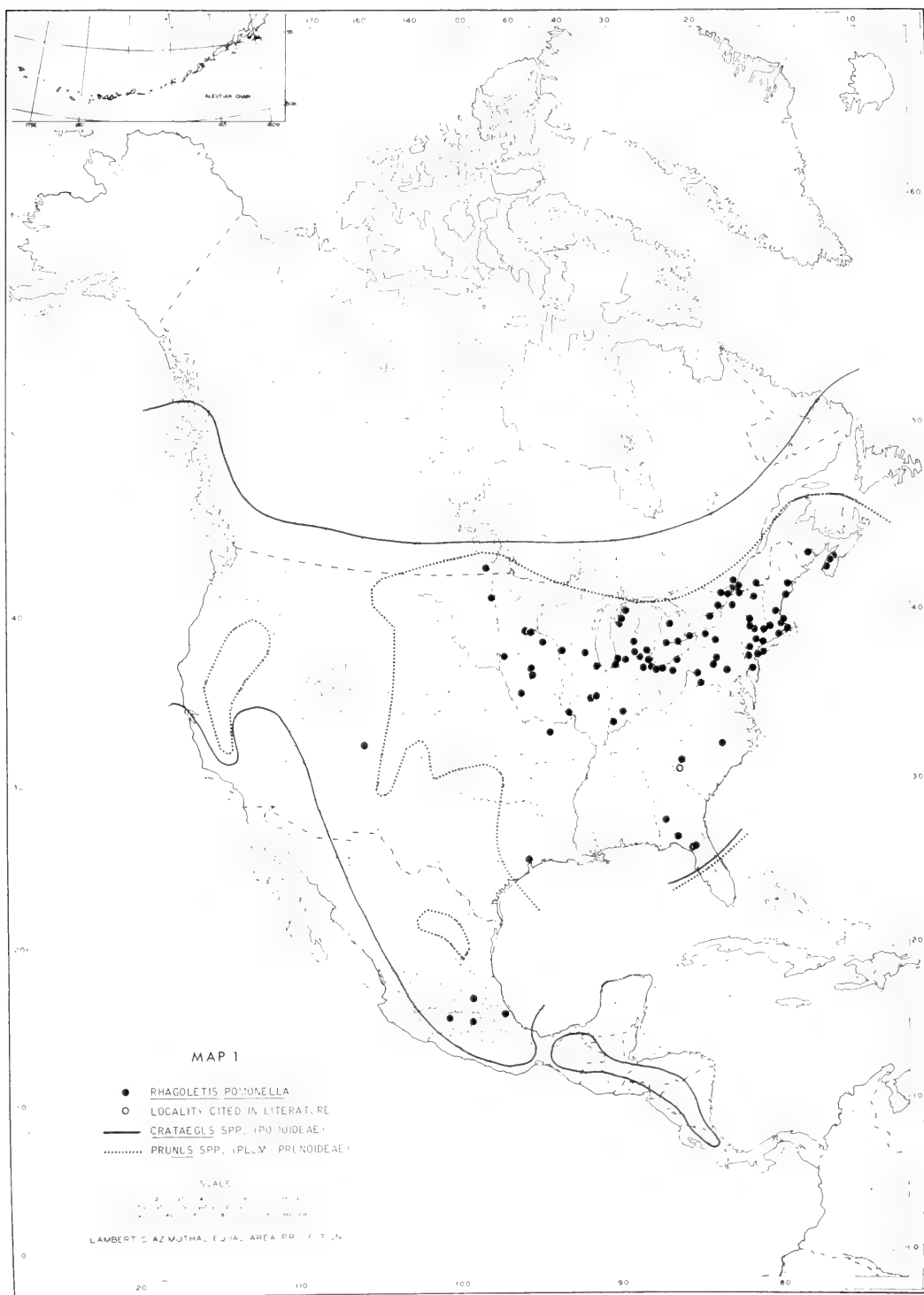
dians who used it as food (Standley and Steyermark, 1946); thus *pomonella* may have been introduced with the fruit.

Rhagoletis zephyria Snow

Rhagoletis zephyria Snow, 1894, Kansas Univ. Quart., 2: 164–165. [Described from 5 ♂ ♂, southern California (leg. Baron) (KU); lectotype ♂ examined, designated by Foote, 1962; also examined: 3 ♂ ♂ (KU), 1 ♂ (MCZ, No. 7724).] —Doane, 1898, Ent. News, 9: 69 (in key, = *pomonella*). —Curran, 1924, Canad. Ent., 56: 62–63 (distinct from *symphoricarpi*). —Benjamin, 1934 (in part), U.S. Dept. Agr. Tech. Bull., 401: 9, 12 (syn. *symphoricarpi* with *zephyria*). —Pickett, 1937, Canad. J. Res. (D), 15: 56–57, figs. 4, 16, 17, 23, 25 (subspecies of *pomonella*). —Foote, 1962, J. Kansas Ent. Soc., 35: 178–179 (lectotype designated).

Rhagoletis pomonella Aldrich, 1905 (in part), Smithson. Misc. Coll., 1444: 607 (in catalog, syn. of *pomonella*). —Aldrich, 1909 (in part), Canad. Ent., 41: 69 (syn. of *pomonella*). —Cresson, 1929 (in part), Trans. Amer. Ent. Soc., 55: 409–410 (syn. both *zephyria* and *symphoricarpi* with *pomonella*).

Rhagoletis symphoricarpi Curran, 1924, Canad. Ent., 56: 62–63. [Holotype ♂ not examined, Victoria, B.C., June 30, 1919, reared from *Symphoricarpos* (W. Downes) (CNC, No. 634); paratypes examined: 2 ♂ ♂ 1 ♀, Victoria, B.C., June 20; 2 ♂ ♂ 1 ♀, June 24; 1 ♂ 1 ♀, June 25, 1919, host *Symphoricarpos* (W. Downes) (CNC, No. 634); 1 ♂, Creston, B.C., no date or leg., host *Symphoricarpos* (CNC, No. 634); 1 ♀, Lytton, B.C., no date or leg., host *Symphoricarpos* (CNC, No. 634).] —Phillips, 1946, Mem. Ent. Soc. Amer., 12: 76–77, figs. 32, 77, 140, 179 (larval morphology, in key).

Diagnosis. R. *zephyria* is sympatric with *pomonella* only in the extreme eastern limits of its range. It can be distinguished from *pomonella* by surstyli shape (Figs. 69, 91; Table 4), ovipositor length (Fig. 21), wing band ratio (Table 5), and its exclusive association in the larval stage with snowberry (*Symphoricarpos*). Surstyli shape and host preference will also distinguish *zephyria* from all other described species in the *pomonella* complex. There is some similarity between *zephyria* and Florida *mendax* in the shape of the surstyli; however, those of *mendax* are more angled

in lateral view (Table 4) and not flared in posterior view (Figs. 91, 94).

Geographical variation. No geographical variation was noted in this species.

Chromosome number and morphology (Fig. 215). The diploid number is 12; the MCA number is 18 as there are three pairs of metakinetic chromosomes, two pairs of acrokinetic rod-shaped chromosomes and a single pair of acrokinetic dot chromosomes. No morphologically differentiated heterochromosomes (XY) or secondary constrictions were observed.

Source of cytological material: *Symphoricarpos* sp., Corvallis, Oregon, July 20, 1961; Forestville, California, Aug. 10, 1961.

Courtship behavior. The courtship behavior of this species was not studied.

Parasites. Opius lectoides (Gahan, 1930) is the only parasite recorded from *zephyria*. It has not been found associated with any other *Rhagoletis* species.

Hosts. R. *zephyria* has only been reared from *Symphoricarpos* (Caprifoliaceae) which is closely related to *Lonicera* (Jones, 1940), a genus infested by several European *Rhagoletis* species. Lathrop and Nickels (1931, 1932) state that *zephyria* has also been found in the fruits of blueberry and whortle berry in the western United States, but give no details regarding the source of their information. R. *tabellaria* is the only species known to infest *Vaccinium* in the West, and I have been unable to confirm the Lathrop and Nickels host record.

Symphoricarpos is almost entirely restricted to North America where 16 species are known. One species has been found in central China (Jones, 1940). There is a continuous distribution of various representatives of this genus over North America ranging from southeastern Alaska to central Guatemala.

R. *zephyria* has been reared from S. *rivularis* Suksdorf (S. *albus* and S. *racemosus* of authors; see Jones, 1940, for discussion of synonymy), whose distribution (Map 2) coincides fairly well with that of *zephyria*.

MAP 2

●   RHAGOLETIS ZEPHYRIA
○   LOCALITIES CITED IN LITERATURE
——   SYMPHORICARPOS SPP.
---------   SYMPHORICARPOS RIVULARIS

SCALE

LAMBERT'S AZIMUTHAL EQUAL-AREA PROJECTION
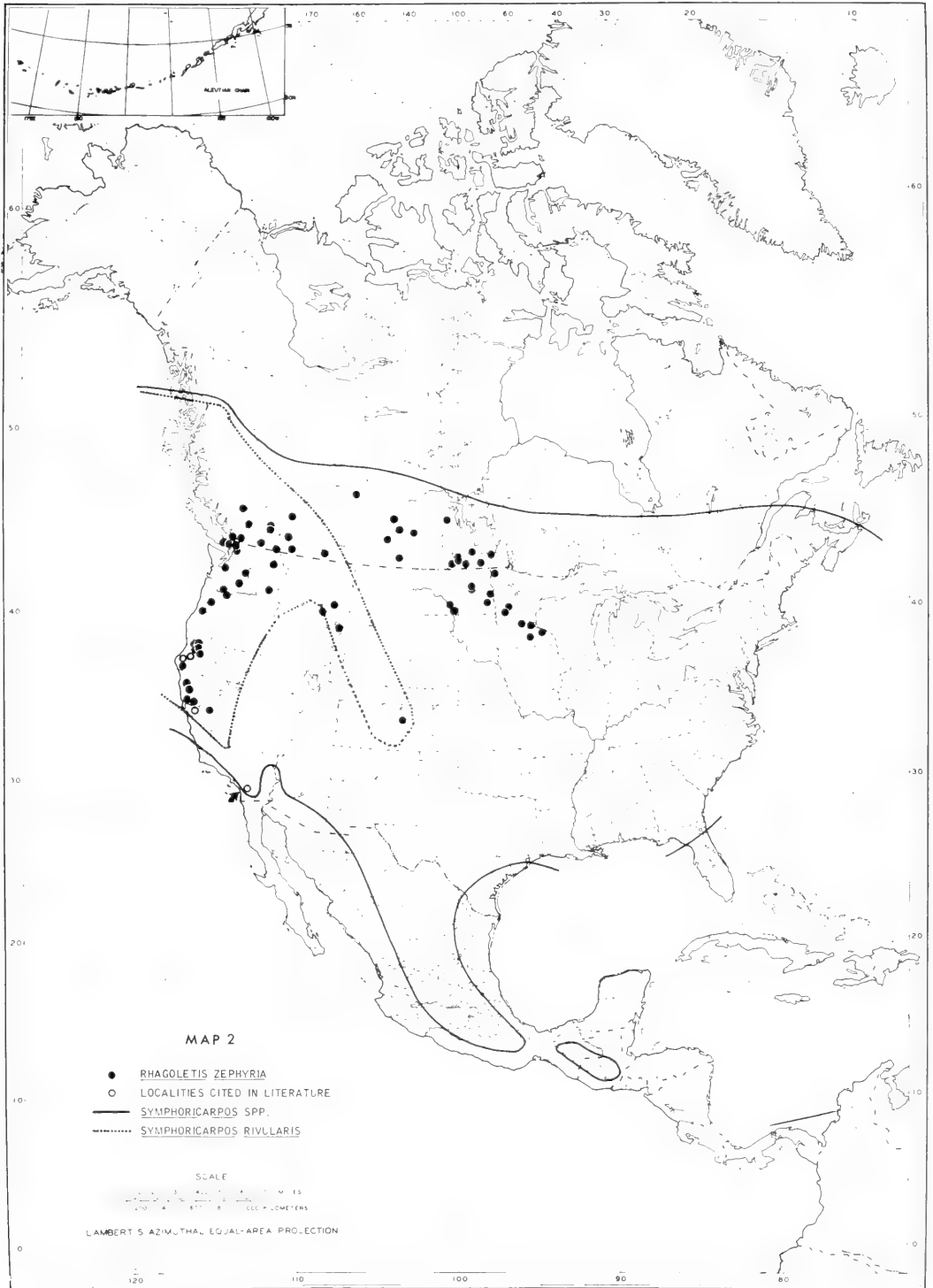
S. rivularis has been introduced and escaped from cultivation over a wide range in eastern North America, a fact which may account for the extension of the range of *zephyria* so far to the east.

Since this fly may infest other *Symphoricarpos* species, the approximate distribution of the genus in North America has also been shown.

Distribution (Map 2). This species ranges from southern British Columbia south to the central and possibly southern highlands of California, and east in southwestern Canada and northwestern United States to Minnesota.

Rhagoletis mendax Curran

Rhagoletis pomonella, —Britton, 1906, Conn. Agr. Expt. Sta. Ann. Rept. (1905), 29: 260 (infesting *Gaylussacia* in Conn.). —Phillips, 1923 (in part), J. New York Ent. Soc., 31: 136 (in cranberries). —Cresson, 1929 (in part), Trans. Amer. Ent. Soc., 55: 409–410 (taxonomic status). —Benjamin, 1934 (in part), U.S. Dept. Agr. Tech. Bull., 401: 9, 12 (taxonomy). —Pickett, 1937, Canad. J. Res. (D), 15: 53–75 (taxonomy, race of *pomonella*). —Phillips, 1946, Mem. Amer. Ent. Soc., 12: 70, figs. 27, 72, 131–132, 174 (larval morphology, in key).

Rhagoletis mendax Curran, 1932, Amer. Mus. Nov., 526: 6, 7. [Holotype ♂ examined (abdomen missing), Maine (A. D. Pickett) (AMNH); allotype ♀ and ♂ paratype examined, same data as holotype.]

Rhagoletis zephyria, —Benjamin, 1934 (in part), U.S. Dept. Agr. Tech. Bull., 401: 9, 12.

R. mendax was originally described by Curran (1932) from *pomonella*-like flies reared from blueberries in Maine. With the exception of Christenson and Foote (1960), current authors have not accepted Curran's recognition of *mendax* as a distinct species. Most entomologists continue to refer to this species only as a distinct race of *pomonella*, even though crossbreeding experiments have clearly shown that these two "races" are reproductively isolated (see Table 2). Moreover, the two species appear ecologically distinct with uninfested blueberries growing in the vicinity of heavily infested apples or hawthorns and

vice versa (Woods, 1915a; Lathrop and Nickels, 1932). *R. pomonella* also has a much more extensive westward range than *mendax*. Blueberries beyond Michigan are not known to be infested by this species. These facts, as well as others already pointed out in the discussion of the *pomonella* group, make it impossible to regard *mendax* as simply a race of *pomonella*.

Diagnosis. *R. mendax* north of Georgia may be distinguished from *pomonella* by the following combination of characters: (1) shorter ovipositor length (Fig. 21); (2) difference in wing band ratios (Table 5); (3) absence of black shading on the posterior surface of femur I; (4) larvae infest fruits of *Vaccinium*.

The problem of separating *mendax* from *cornivora* is more difficult. No crossbreeding experiments have been made between these two species. In Ontario, however, *Cornus amomum* is heavily infested with *cornivora*, but Hall (1943) was unable to find blueberries infested, indicating a definite host preference between the two species. There is probably a significant difference in ovipositor length but the number of *cornivora* specimens available for study was not sufficient to make a statistical comparison. The male genitalia may also furnish useful characters for separation as the surstyli ratio in *mendax* is much smaller than in *cornivora* (Table 4). Again, it should be stressed that the number of specimens examined was small. The allopatric species, *zephyria*, may be distinguished on the basis of surstyli shape (Figs. 67, 69, 91, 93) and host preference.

In Florida, *mendax* can be distinguished from *cornivora* and *pomonella* on the basis of host preference and by the shape (Fig. 70) and angle of the male surstyli (Table 4). Females, however, possess no morphological characters that can be used to separate them from females of the other two sympatric species.

Geographical variation. There is a distinct difference in the male genitalia between the Florida and northeastern popula-

Table 6. Members of the family Rosaceae recorded as hosts of *R. pomonella*. L = larvae only observed; A = identification confirmed by rearing larvae to adult stage.

Subfamily	Genus	Species	Locality	Author(s)	Remarks
Pomoideae	*Crataegus*	*punctata* Jacq.	N.Y.	Wellhouse 1922	A
		pedicellata Sarg. (= *albicans*)	N.Y.	Wellhouse	A
		Brainerdi Sarg.	N.Y.	Wellhouse	A
		pruinosa (Wendl.) K. Koch	N.Y.	Wellhouse	A
		macrosperma Ashe	N.Y.	Wellhouse	A
		melanocarpa ?	N.Y.	Glasgow 1933	A
		maloides ?	Fla.	Nicholson 1929–30	A
		spp.	E U.S., SE Can.	O'Kane 1914	A
			Central Mex.	Bush (unpublished)	A
Pomoideae	*Pyrus*	*Malus* L.	E U.S., SE Can.	Authors 1868–1963	A
			Central Mex.	Bush (unpublished)	A
		baccata L.	Ont.	O'Kane 1914	A
		crabapple × *Malus*	N.H., Mich.	O'Kane 1914	A
		communis L.	Conn., Me.	Porter 1928	L
Pomoideae	*Aronia*	*arbutifolia* (L.) L.	Fla.	Benjamin 1934	A
		melanocarpa (Michx.)	Me.	Lathrop and Nickels 1932	L
Pomoideae	*Amelanchier*	*Bartramiana* (Tausch) Roemer	Me.	Lathrop and Nickels 1932	L
Pomoideae	*Cotoneaster* (*Pyracantha*)	sp. ?	Tex.	USDA	A
Prunoideae	*Prunus*	*angustifolia* Marsh.	Fla.	Benjamin 1934	A
		umbellata Ell.	Fla.	Benjamin	A
		cultivated plum	N.Y., N.B.	Herrick 1920	A

tions of *mendax*. On this basis, Benjamin (1934) regarded the Florida *Vaccinium*-infesting population to be synonymous with *zephyria*, an allopatric species infesting an entirely different host. The male genitalia do bear some resemblance, but the distribution of the two species and difference in host requirements would rule out a close relationship. Divergence of the Florida *mendax* from the northeastern population probably occurred sometime during the Pleistocene when peninsular Florida was isolated from the mainland as a chain of islands. Since both populations of *mendax* utilize the same hosts, it seems inadvisable to consider the Florida form as a distinct species in the absence of crossing experiments and more detailed knowledge of the biology and distribution of both populations.

Two males from Bobcaygeon, Ontario (in the CNC), have been tentatively assigned to *mendax*. The genitalia of one specimen have been examined and the surstyli are very similar in shape to those found in Florida *mendax*. There are no records of *mendax* infesting blueberries in Ontario. In view of these facts, the identification of these specimens is in doubt.

Chromosome number and morphology (Fig. 216). The diploid number is 12; the MCA number is 18 as there are three pairs of metakinetic chromosomes, two pairs of rod-shaped acrokinetic chromosomes, and a single pair of acrokinetic dot chromosomes. No morphologically differentiated heterochromosomes (XY) or secondary constrictions were observed.

Source of cytological material: *Vaccinium* spp., Northfield, New Hampshire, Aug.

TABLE 7. SPECIES OF ERICACEAE FOUND INFESTED BY *R. mendax*. REMARKS: L = LARVAE ONLY OB-
SERVED; A = IDENTIFICATION CONFIRMED BY REARING LARVAE TO ADULT STAGE. TAXONOMIC TREATMENT
OF HOST PLANTS FOLLOWS CAMP (1941, 1945) AND WOOD (1961).

GENUS	SUBGENUS OR SECTION	SPECIES	LOCALITY	AUTHOR(S)	REMARKS
Vaccinium	*Cyanococcus*	*angustifolium* Ait. (= *pennsylvanicum* of authors)	Me., N.J.	Lathrop and Nickels 1932; Woods 1915a	A
		canadense Kalm	Me.	Woods 1915a	A
		corymbosum L.	Me., N.H., N.J.	Woods 1915a; O'Kane 1914	A
		pallidum Ait.	N.J.	teste Marucci	A
		spp.? (blueberries)	Mich.	Anonymous 1963	A
		Formosum Andr. (prob. *fascatum* Ait.)	Fla.	Nicholson 1929–30	L
	Batodendron	*arboreum* Marsh.	Fla.	Benjamin 1934	A
	Vitis-idaea	*vitis-idaea* L.	Me.	Lathrop and Nickels 1932	L
	Oxycoccoides	spp.? (cranberries)	N.S.	Phillips 1923	L(A?)
				Pickett and Neary 1940	L
				Bush (unpublished)	A
Gaylussacia	*Decamerium*	*baccata* (Wang.) K. Koch	Conn., Me., N.H.	Britton 1906; Woods 1915a; teste Marucci	A
		frondosa (L.) T.&G.	N.J.	teste Marucci	A
		dumosa (Andr.) T.&G.	N.J.	teste Marucci	A
Gaultheria	*Gaultheria*	*procumbens* L.	Me.	Lathrop and Nickels 1932	L

27, 1960; Yarmouth, Nova Scotia, Sept. 7, 1962; vicinity of Wilcox, Florida, June 29, 1962.

Courtship behavior. The courtship behavior of this species was not studied.

Parasites. The following parasites have been reared from *mendax* in Maine: *Opius melleus* Gahan (=*Biosteres rhagoletis* Richmond of Woods, 1915b) and *O. richmondi* Gahan (Lathrop and Nickels, 1932) (Braconidae). Apparently *O. melleus* is by far the more frequently encountered parasite. Parasitism averages about 10.7 per cent.

It has also been stated that adults of *O. melleus* parasitizing *mendax* are much smaller than *O. melleus* which parasitize *pomonella* (Lathrop and Newton, 1933). This suggests that two species of *Opius* may be associated with *mendax* and *pomonella*.

Hosts. Adults of *mendax* have been reared only from *Vaccinium* and *Gaylus-sacia* (Ericaceae). Larvae identified as *mendax* have also been found in *Gaultheria procumbens* L. (wintergreen; Ericaceae), but adults have never been recovered. Table 7 outlines the species of plants with which *mendax* has been found associated. There is an apparent preference for *Vaccinium* and *Gaylussacia* whose fruits are similar in many respects. Wintergreen and cranberries do not appear to be suitable hosts for this species and I have examined only a few specimens reared from the latter host.

Host distribution is based on Camp (1941, 1945).

Distribution (Map 3). *R. mendax* is primarily restricted to northeastern United States and southeastern Canada. It has been reared from blueberries as far west as Michigan, and I have examined a single damaged specimen from Milwaukee, Wis-

MAP 3

- **RHAGOLETIS MENDAX**
- ○ LOCALITIES CITED IN LITERATURE
- —·—·— VACCINIUM (CYANOCOCCUS) SPP.
  AND GAYLUSSACIA SPP.
- ———— VACCINIUM (BATODENDRON) ARBOREUM

SCALE

LAMBERT S AZIMUTHAL EQUAL-AREA PROJECTION
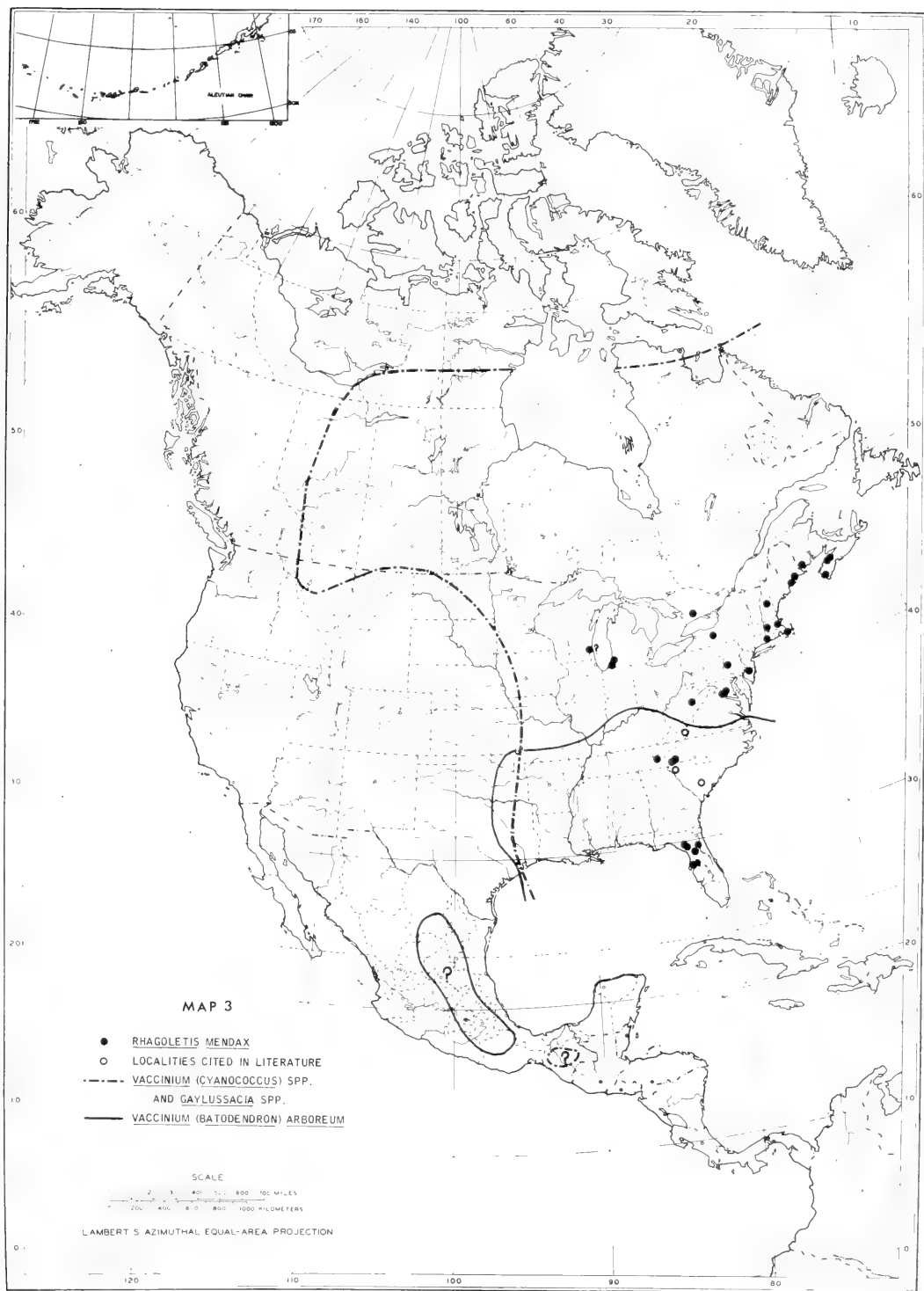
consin, which I am tentatively regarding as conspecific. The second morphologically distinct population occurs in Florida and may be coextensive with the northern population, but insufficient collecting makes it impossible to establish its range with certainty.

Rhagoletis cornivora new species

Types. Holotype ♂, Lincoln, Mass., larva collected Sept. 10, 1962, ex *Cornus stolonifera* (G. L. Bush) (MCZ, No. 30828); paratypes: 3 ♂ ♂ 4 ♀ ♀, same data as holotype (MCZ, No. 30828).

Hall (1938, 1943) has shown through crossing experiments that *cornivora* is reproductively isolated from *pomonella* (Table 2). Apparently *cornivora* has difficulty ovipositing in apple and the larvae have not been reared from this fruit in forced oviposition experiments. Pickett (vide Hall, 1938) also noted consistent morphological differences between the surstyli of *cornivora* and other members of the *pomonella* group. He did not, however, regard them as important enough to consider the *Cornus*-infesting race a distinct species. Because the two sympatric "host races" are reproductively isolated and show morphological differences associated with host preference, it is necessary to consider the *Cornus* race a distinct species.

Two populations of *cornivora* showing slight but probably significant morphological differences in male and female genitalia have been found in Florida and the Northeast (see *Geographical variation*). These two populations are considered here to be conspecific. Eventually, when more biological data are available, they may prove to be different species.

Diagnosis. R. *cornivora* may be distinguished from the other sympatric members of the *pomonella* group (*mendax* and *pomonella*) north of Georgia by the surstyli shape and ratio (Table 4; Figs. 68, 92), ovipositor length (Fig. 21), and the host preference for *Cornus* spp. Also there is a slight difference in the morphology of

the meiotic chromosomes of *cornivora* and the other members of this group which may be used to identify the species if living material is available (see *Chromosome* section). Females of the Florida population of *cornivora* cannot be distinguished from *mendax* or *pomonella* without host data as there is considerable overlap in ovipositor length of all three species. There are no differences in the male genitalia of *cornivora* and *pomonella*.

Geographical variation. There is some variation between the Florida and northeastern populations of *cornivora* in ovipositor length and surstyli ratio. The northeastern populations have been reared from three species of *Cornus,* while Florida representatives have been reared only from *C. florida*. Also the trend toward reduction in size noted in *pomonella* is reversed in this species: adults of *cornivora* from Florida are considerably larger than those reared from *Cornus* in northeastern United States. This may be a true case of geographical variation, or perhaps two distinct species are involved. The answer will have to await further biological data.

Chromosome number and morphology (Fig. 217). The diploid number is 12; the MCA number is 18 in the female and 19 in the male. The male karyotype consists of a submetakinetic Y chromosome slightly longer than the acrokinetic X chromosome, a single pair of acrokinetic autosomes, three pairs of metakinetic autosomes, and a pair of dot acrokinetic autosomes. The female karyotype has a pair of acrokinetic X chromosomes, a single pair of acrokinetic autosomes, three pairs of metakinetic autosomes, and a pair of dot acrokinetic autosomes. No secondary constrictions were noted. The presence of the Y chromosome in the male was confirmed through a study of meiotic and spermatogonial figures in adult testes.

Source of cytological material: *Cornus stolonifera*, Lincoln, Mass., Sept. 13, 1960.

Courtship behavior. The courtship behavior of this species has not been studied.

MAP 4

- ● RHAGOLETIS CORNIVORA
- —— CORNUS FLORIDA
- .... CORNUS STOLONIFERA, C. CANADENSIS,
       AND C. AMOMUM

SCALE

LAMBERT'S AZIMUTHAL EQUAL-AREA PROJECTION
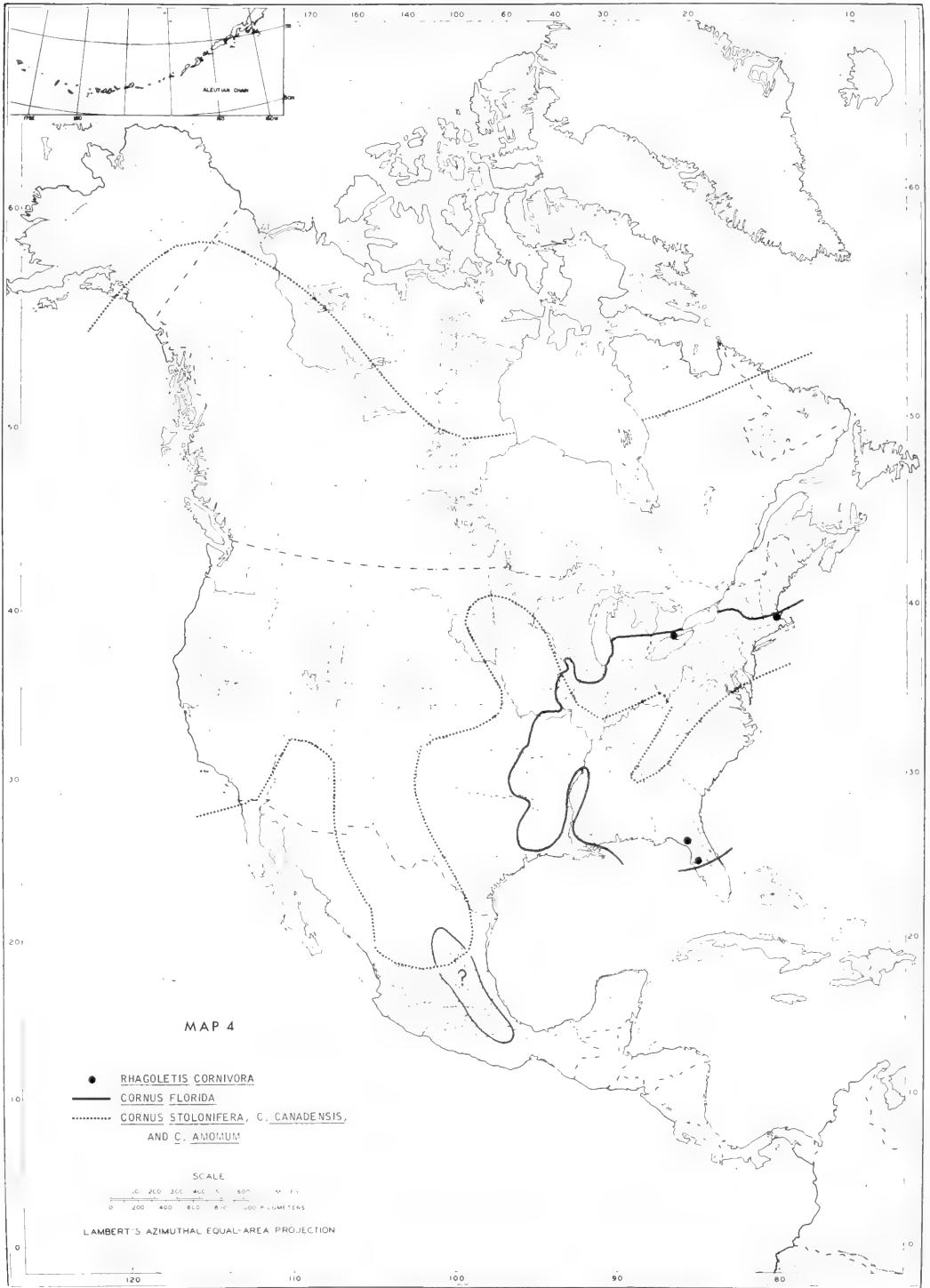
Hosts. R. *cornivora* has been reared from the fruits of the following host plants: *Cornus canadensis* L. in Maine (Lathrop and McAlister, 1931), *C. amomum* Mill. in Ontario (Hall, 1938, 1943), *C. stolonifera* Michx. in Massachusetts, and *C. florida* L. in Florida (Benjamin, 1934). R. *cornivora*-like larvae have also been found in the fruits of *C. florida* on Plummer's Island, Maryland, indicating that this plant may serve as a host over most of its range. It is not known if R. *cornivora* occurs on the Mexican subspecies of *C. florida*.

Distribution. Map 4 shows the inclusive distribution of the three northeastern species of *Cornus* infested by *cornivora*. The distribution of *C. florida* is also outlined showing the isolated subspecies in Mexico. Floristic connections between certain xero-mesophytic plants were probably made and broken repeatedly between eastern North America and Mexico during the Pleistocene (Dressler, 1954; Martin and Harrell, 1957). *C. florida* therefore probably had a continuous distribution before and possibly during some parts of the Pleistocene. The presence of *cornivora* in Mexico could furnish clues to the time of origin of this species. Distribution of the host plants is based on Rickett (1944, 1945, 1950).

CINGULATA SPECIES GROUP

Three species and one subspecies of *Rhagoletis* have been found associated with wild and cultivated cherries (*Prunus*): R. *cingulata* (Loew), the eastern cherry fruit fly; R. *cingulata indifferens* Curran, the so-called western subspecies of the cherry fruit fly; and R. *fausta* (Osten Sacken), or black cherry fruit fly are native to North America. The third species, R. *cerasi* (Linn.) is the common European cherry fruit fly and the type of the genus. On the basis of host preference, several authors have referred these three species to the same species group or attested to their close relationship. However, on morphological grounds this is an artificial grouping and does not represent true relationships. As

it is now conceived, the *cingulata* group consists of four native North American species, two associated with the plant genus *Prunus* (Rosaceae) and the other two infesting fruits of *Osmanthus* and *Chionanthus* (Oleaceae). R. *cerasi*[9] and R. *fausta* are not closely related and should be placed in separate species groups.

Prior to the present revision, these species were generally considered to be only host races or subspecies (Cresson, 1929; Benjamin, 1934; Pickett, 1937; Blanc and Keifer, 1955). Although the species are admittedly very similar, there are several biological reasons for considering them distinct.

In sympatric populations of the *cingulata* group (i.e., *cingulata*, *osmanthi*, and *chionanthi*) consistent morphological differences correlated with host preferences are evident in the dimensions of the ovipositor and wing patterns. These differences could not be maintained in sympatric populations which were not reproductively isolated.

The two allopatric populations associated with the fruits of several *Prunus* species should also be considered distinct. The morphological differences between *indifferens* and *cingulata* are as great or greater than those existing between the sympatric populations of *cingulata* and the two olive-infesting species in Florida. Therefore, there is no reason for considering *indifferens* a subspecies of *cingulata* as it has been in the past.

Diagnosis. The *cingulata* group is easily distinguished from all other *Rhagoletis* species groups on the basis of the following combination of characters: (1) the wing pattern bears a distinct apical fork which may be modified in having the anterior prong of the fork reduced to an apical spot (Figs. 203–204); (2) the surstyli have apical tufts of longer setae (i.e., Figs. 79–82), and the aedeagal tip has a fluted rake-like appendage (Figs. 118–121); (3) the dor-

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[9] For comparative purposes the following morphological features have been illustrated for R. *cerasi*: head (Fig. 39); male genitalia (Figs. 77, 112, 122); spermathecae (Fig. 172); wing pattern (Fig. 211).

sum is dark brown to black and covered by cream to light yellow pollinose microtrichia and decumbent setae arranged in four ill-defined rows; the outer row reaches from just behind the outer scapulars to an imaginary line drawn between the posterior pair of posterior supraalars; the inner rows reach from the inner scapulars to a point just anterior to the prescutellars.

Certain characteristics of this group suggest a relationship with the *ribicola* group. The spermathecae of members of the *cingulata* group closely resemble those of *ribicola*, while the wing pattern of the latter could be easily derived from that of *cingulata* by simply eliminating the anterior arm of the apical fork. The wing pattern of *berberis* could be derived from that of *cingulata* by eliminating the posterior arm of the fork.

Rhagoletis cingulata (Loew)

Ortalis cerasi, —Harris, 1835, Insects, *In* Hitchcock, Catalogue of Animals and Plants in Massachusetts, pp. 33–82 (probably refers to *cingulata*).

Trypeta cingulata Loew, 1862, Smithson. Misc. Coll., 6: 63, 76–77, pl. 2, fig. 11. [Type examined: ♀, "Middle States" (MCZ, No. 13299).]

Trypeta (*Rhagoletis*) *cingulata*, —Loew, 1873, Smithson. Misc. Coll., 8: 263, 329, pl. 10, fig. 11 (notes type from middle states; Long Branch, N.J.).

Rhagoletis cingulata, —Doane, 1898, Ent. News, 9: 69 (in key). —Bezzi, 1911, Boll. Lab. Zool. Portici, 5: 15 (in key). —Illingworth, 1912, New York (Cornell) Agr. Expt. Sta. Bull., 325: 191–204 (biology, control, technical description). —Phillips, 1923, J. New York Ent. Soc., 31: 35, fig. 22, pl. 18 (in key, description, wing figured). —Cresson, 1929, Trans. Amer. Ent. Soc., 55: 408, pl. 16, fig. 6 (adult taxonomy and redescription). —Curran, 1932, Amer. Mus. Nov., 526: 6, 7 (taxonomy, comparison with *R. indifferens*). — Benjamin, 1934, U.S. Dept. Agr. Tech. Bull., 401: 13–14, 61, fig. 12 (taxonomy, biology of larva and adult). —Pickett, 1937, Canad. J. Res. (D), 15: 60 (genitalia). —Phillips, 1946, Mem. Amer. Ent. Soc., 12: 26, 65–66, figs. 22, 67, 122, 123, 169 (larval morphology, in key). —Frick, Simkover, and Telford, 1954, Washington Agr. Expt. Sta. Tech. Bull., 13: 1–66 (control, biology, intra- and interspecific relationships). —Blanc and

Keifer, 1955, Calif. Dept. Agr. Bull., 44: 77–88, 2 figs. (status of *R. indifferens* and *R. cingulata*).

Diagnosis. The presence of one or more of the following features is usually adequate to distinguish *cingulata* from *indifferens*: (1) an apical ovoid or triangular yellow spot on the posterior margin of tergite V in the male (Fig. 49); (2) an apical fuscous spot on the wing completely separated from the apical band by a hyaline area in most individuals (Table 8); (3) concolorous yellow prothoracic coxa (in *indifferens* black shading is always present on the posterior surface of prothoracic coxa); (4) yellowish orange to light yellow epandrium. No significant differences in the length of the ovipositor or in the length/width ratio, as reported by Blanc and Keifer (1955), were found between these two species.[10]

The characters that distinguish *cingulata* from the olive-infesting species in Florida are not as clear-cut. Accurate identification can only be made on a population basis, or on a single specimen if it is accompanied by suitable host data. The following combination of characters may be used to separate Florida populations of *cingulata* from those of *chionanthi* and *osmanthi*: (1) fuscous apical spot present on wing (Table 8); (2) ovipositor length/width ratio averaging 6.0 (4.2–7.9); (3) ovipositor length averaging 0.85 mm (.79–.93) (see Fig. 18); (4) all head and body measurements smaller than olive-infesting species as shown in Tables 9A–9B; (5) larvae infest fruits of black cherry (*Prunus serotina*).

There is apparently little or no overlap in the ovipositor length of *cingulata* and *osmanthi*. There may be considerable difficulty, however, in separating *cingulata* from *chionanthi* without an adequate number of specimens. As a rule, the olive infesting

[10] Mr. Blanc has kindly loaned me the specimens used in making the measurements referred to in the 1955 paper. I obtained the following measurements: *cingulata* 5.8:1, n = 7; *indifferens* 6.1:1, n = 30, as compared with those of Blanc and Keifer: *cingulata* 5.6:1, *indifferens* 7.5:1.

TABLE 8. FREQUENCY OF APICAL WING SPOT IN THE *cingulata* SPECIES GROUP. A SPOT WAS COUNTED ONLY IF IT WAS COMPLETELY SEPARATED FROM THE APICAL CROSSBAND BY A HYALINE AREA. THOSE FORKS WHICH WERE CONSTRICTED AT THE BASE BUT STILL JOINED TO THE APICAL BAND BY A FUSCOUS REGION WERE COUNTED AS A FORKED PATTERN.

SPECIES	n ♂♂	PER CENT ♂♂ WITH APICAL SPOT	n ♀♀	PER CENT ♀♀ WITH APICAL SPOT
R. cingulata (New York)	95	75.8	48	66.7
R. cingulata (Michigan)	42	71.4	37	59.5
R. cingulata (Penn.)	19	63.2	24	83.3
R. cingulata (Florida)	38	65.8	45	84.4
R. indifferens (all populations)	494	1.4	245	3.2
R. osmanthi (Florida)	26	0	34	0
R. chionanthi (Florida)	12	0	26	0

species are somewhat more yellow than *cingulata*, particularly on the tergites.

Description. Body and wing measurements in Tables 9A–9B. *Head* (Fig. 32): lower two-thirds of postcranium with transverse dark brown stripe, somewhat reduced or absent in specimens from Florida. Frontalia, face, genae, lower two-thirds of postgenae, gulamentum, and mentum yellowish orange; postorbital regions, parafacialia and parafrontalia slightly lighter yellow. Postocellars and genal bristles yellow; gular bristle weak or undifferentiated; all other major bristles black; 8–15 postorbitals. *Thorax*: dorsum covered with white decumbent setae and white pollinose microtrichia arranged in two broad well defined rows, each subdivided into two less distinct rows. Dorsocentrals located on line drawn between anterior supraalars. Normally two pairs pale yellow scapular bristles, both sometimes doubled with supernumeraries

arranged in tandem behind long normal bristles. Pleural and sternopleural bristles brownish black to black, propleuron sometimes tinted with yellow in specimens from southern part of range. Usually only one but sometimes two mesopleural bristles, the second, when present, usually small (24 per cent males and 26 per cent females of all specimens examined had weak to moderately well developed lower mesopleural bristles). Notopleural stripe cream, scutellar spot cream reaching from below apex anteriorly to just before a line drawn between bases of basal scutellar bristles; lateral margins passing through or just outside base of apical scutellars. Postscutellum brownish black to black; halteres lemon yellow. *Legs*: color highly variable. Coxa I, all trochanters, tibiae, and tarsal segments yellowish orange. Femur I usually yellowish orange, sometimes with brownish black tinge along posterior surface; dorsal rows of erect to semierect long bristles yellowish orange, postventral row black. Femur II entirely yellowish orange or with slightly denser black markings on posterior surface than femur I; row of poorly differentiated short black semierect setae on anterior surface of femur II. Femur III mostly yellowish orange or heavily marked with black, particularly along posterior surface. Tibia III with a single row of semierect well developed brown setae on anterior outer surface. *Wing*: pattern variable, Figure 203 representing most frequently encountered condition,[11] with upper arm of apical fork broken by hyaline area leaving small apical spot (see Table 8 for frequencies). Figure 204 represents other extreme of pattern with an apical fork. Medial band not joined to basal or subapical bands. Usually single seta dorsally at junction of R_{2+3} and R_{4+5}; R_{4+5} bare. Anal cell strongly pointed. Crossvein r-m at about midpoint between M_3 and m.

[11] Cresson (1929) illustrates the wing of *cingulata* (pl. 16, fig. 6) without a basal crossband. This is undoubtedly an error as I have never seen a specimen of any species in the *cingulata* group which does not bear a conspicuous basal crossband.

	R. [.....] Fla.	R. [.....] N.Y.-Mich.	R. [.......]	R. [.......]	R. [.....]
	10	10		10	5
HL	.75±.008 (.72-.79)	.88±.015 (.82-.96)	.82±.015 (.72-.91)	.89±.01? (.78-.96)	.87 (.83-.??)
HA	1.32±.017 (1.23-1.40)	1.47±.018 (1.34-1.54)	1.33±.032 (1.09-1.60)	1.51±.027 (1.34-1.64)	1.50 (1.35-1.67)
IO	1.10±.012 (1.05-1.16)	1.23±.015 (1.13-1.28)	1.0?±.02? (.87-1.21)	1.27±.021 (1.19-1.38)	1.27 (1.14-1.41)
FW	.6?±.008 (.65-.72)	.75±.010 (.6?-.80)	.57±.014 (.??-.73)	.80±.012 (.74-.88)	.7? (.6?-.83)
FL	.92±.011 (.86-.95)	1.01±.01? (.90-1.00)	.8?±.022 (.72-1.00)	1.05±.018 (.96-1.14)	1.03 (.93-1.13)
FW	.4?±.005 (.42-.45)	.50±.008 (.44-.53)	.46±.010 (.36-.53)	.46±.009 (.43-.51)	.46 (.40-.53)
	.41±.005 (.39-.43)	.46±.002 (.42-.48)	.43±.011 (.35-.53)	.48±.007 (.43-.51)	.45 (.40-.52)
	.5?±.009 (.56-.61)	.63±.017 (.61-.76)	.?0±.01? (.50-.67)	.6?±.013 (.62-.75)	.67 (.62-.77)
GA	.16±.003 (.15-.18)	.21±.007 (.18-.25)	.1?±.007 (.13-.24)	.22±.008 (.1?-.26)	.1? (.17-.22)
	1.68±.016 (1.5?-1.76)	1.91±.025 (1.76-2.03)	1.68±.040 (1.55-1.?0)	1.86±.0?? (1.65-1.98)	1.8? (1.70-2.13)
	10	10	10	10	5
W	2.78±.021 (2.65-2.88)	3.15±.049 (2.93-3.43)	3.0?±.0?? (2.61-3.50)	3.0?±.0?? (2.88-3.34)	3.08 (2.78-3.36)
WA	1.47±.020 (1.37-1.57)	1.65±.041 (1.41-1.83)	1.6?±.05? (1.31-1.83)	1.62±.037 (1.34-1.73)	1.71 (1.53-1.93)

Table 9A. Body and wing measurements of males of the *cingulata* species group. Figures represent mean, standard error, and range.

	[.....] Fla.	R. [.....] N.Y.-Mich.	[.........]	R. [.......]	R. [.....]
	1?	?0			
HL	.7?±.014 (.72-.86)	.92±.017 (.83-.99)	.8?±.016 (.74-.97)	.9?±.013 (.83-1.03)	.9?±.017 (.8?-1.00)
HA	1.36±.032 (1.19-1.50)	1.55±.006 (1.44-1.63)	1.48±.030 (1.12-1.60)	1.64±.031 (1.41-1.74)	1.5?±.04? (1.??-1.72)
HB	1.10±.021 (1.00-1.1?)	1.30±.013 (1.22-1.36)	1.21±.025 (.94-1.33)	1.3?±.02? (1.22-1.50)	1.2?±.02? (1.15-1.42)
FW	.70±.015 (.61-.76)	.79±.007 (.74-.82)	.75±.01? (.58-.81)	.8?±.015 (.7?-.92)	.80±.01? (.70-.90)
FL	.9?±.022 (.81-1.02)	1.08±.014 (1.00-1.11)	1.00±.023 (.76-1.09)	1.14±.021 (.9?-1.2?)	1.0?±.02? (.9?-1.1?)
FW	.45±.011 (.38-.48)	.54±.008 (.49-.57)	.51±.011 (.39-.57)	.50±.010 (.43-.52)	.47±.015 (.3?-.5?)
	.43±.006 (.41-.45)	.48±.008 (.43-.51)	.46±.010 (.36-.53)	.51±.00? (.45-.56)	.4?±.00? (.44-.53)
	.61±.017 (.55-.70)	.70±.013 (.62-.75)	.6?±.014 (.50-.73)	.74±.016 (.65-.80)	.6?±.01? (.61-.78)
GA	.18±.005 (.16-.20)	.22±.002 (.18-.24)	.22±.008 (.15-.26)	.2?±.008 (.18-.26)	.21±.00? (.17-.2?)
	1.81±.046 (1.52-1.98)	2.0?±.0?7 (1.98-2.23)	1.9?±.047 (1.7?-2.10)	2.0?±.048 (1.87-2.26)	1.9?±.06? (1.62-2.2?)
	1?	1?		1?	
W	3.0?±.054 (2.75-3.30)	3.6?±.021 (3.50-3.76)	3.47±.059 (3.07-3.68)	3.56±.085 (2.84-3.78)	3.3?±.07? (2.9?-3.??)
WA	1.6?±.034 (1.41-1.77)	1.9?±.0?? (1.90-2.01)	1.82±.034 (1.60-1.93)	1.9?±.060 (1.4?-2.1?)	1.8?±.044 (1.?4-2.0?)

Table 9B. Body and wing measurements of females of the *cingulata* species group. Figures represent mean, standard error, and range.

Abdomen: variable in color. In northeastern representatives all segments usually black in both sexes with whitish pollinose band of silvery microtrichia along posterior margin of tergites II–IV in male (Fig. 49), and II–V in female as in *indifferens* (Fig. 52); tergite V in male and tergite VI in female with small semicircular yellow mark on posterior margin. Florida specimens with greatly reduced black areas replaced with yellow leaving small irregular brownish black spots on either side of medial line (Fig. 50). *Genitalia: male* — epandrium and surstyli yellowish orange (Figs. 79, 111); genital ring membrane normal; phallic apodeme curved; aedeagus (Fig. 118) with setulose finger-like apical appendage; vesica smooth; ejaculatory apodeme normal (Fig. 152). *Female*— variation in ovipositor length shown in Figure 18; ovipositor tip with two pairs minute preapical setae; ovipositor sheath brownish black to black. Two twisted cylindrical spermathecae covered with small appressed scale-like papillae (Fig. 168); three spermathecal ducts.

Geographical variation. There are three apparent trends of geographical variation in this species. Adult specimens in Florida tend to be smaller than those from the Northeast. Figure 18 illustrates the differences in ovipositor lengths between allopatric and sympatric species in the *cingulata* complex. The second trend is toward a reduction in the black coloration on the abdomen and legs in specimens from the extreme southern parts of the range of *cingulata*. These two tendencies are apparently associated with a shift from a humid to a more xerophytic environment.

There is also a significant difference in the frequency of the apical wing spot between Florida and New York–Michigan specimens (Table 8). The frequency of spotting is considerably higher in females of the Florida population than in those from New York and Michigan.

This may represent a case of character displacement (for details see Brown and Wilson, 1956, and Mayr, 1963). Since the wing pattern is an important component in courtship displays and species recognition, the presence of a closely related congener may cause the pattern to diverge in the zone of sympatry. *R. cingulata* has no closely related species in the Northeast, and the frequency of the apical wing spot may therefore be less important than in Florida where this species and *chionanthi* are found sympatrically during the same season.

The high frequency of the apical wing spot in *cingulata* females from Pennsylvania indicates that the closely related *chionanthi* may also occur this far north, although no specimens referable to this species have been reported from that area. *Chionanthus americanus*, the host of *chionanthi*, reaches its northernmost limit in southeastern Pennsylvania.

Chromosome number and morphology (Fig. 224). The diploid number is 12; the MCA number is 22 as there are five pairs of metakinetic chromosomes and a single pair of acrokinetic dot chromosomes. No morphologically differentiated heterochromosomes (XY) or secondary constrictions were observed.

Source of cytological material: *Prunus serotina*, Plum Island, Mass., Sept. 10, 1960; Lincoln, New Hampshire, Aug. 27, 1960.

Courtship behavior. The courtship behavior of *cingulata* has not been studied.

Parasites. The only parasite that has been reared from *cingulata* is *Opius ferrugineus* Gahan (Braconidae) (Middlekauff, 1941; Frick et al., 1954). There are probably several other parasites of this species as Frick et al. (1954) have listed nine new ones infesting the sibling species *indifferens* in northwestern United States.

Hosts. A summary of the history leading to the discovery of the hosts of *cingulata* has been presented recently by Frick et al. (1954), and therefore will not be repeated in detail.

The native hosts of this species were not known until about thirty years after it had been first reported as a pest of cultivated cherry. Farleman (1933) found the eastern

cherry fruit fly infesting black cherry, *P. serotina* Ehrh., choke cherry, *P. virginiana* L., and pin cherry, *P. pennsylvanica* L. in Michigan. Glasgow (1933) reported the occurrence of *cingulata* on *P. serotina* in New York, but was unable to rear adults from fruits of either of the other two *Prunus* species even though he frequently observed *cingulata* ovipositing in the fruits of *P. virginiana*. He concluded that *P. virginiana* would only rarely serve as a host for *cingulata*, and could not be regarded as the preferred host for this species in New York. In Massachusetts and New Hampshire, I have never been able to find *cingulata* larvae in *P. virginiana* even when this species was growing among heavily infested *P. serotina*.

I have examined a long series of specimens of *cingulata* from Michigan bearing labels "*P. pennsylvanica*," but it is not clear whether the specimens were reared or simply swept from the tree. Also the identification of the host may be in error. *R. fausta* which normally infests *P. pennsylvanica*, is common in Michigan and it is doubtful that *cingulata* would infest this species of cherry under competitive conditions with *fausta*.

Other hosts of *cingulata* include most of the introduced cultivated cherries such as *P. mahaleb* L. (Mahaleb cherry), *P. avium* (L.) (Mazzard or sweet cherry), and *P. cerasus* L. (sour, Morello, or pie cherry) (Frick et al., 1954).

Distribution (Map 5). *R. cingulata* probably covers most of the range of its principal native host plant, *P. serotina*, in eastern North America. I have never found the fruits of *P. serotina* infested in Mexico, and it is doubtful that *cingulata* occurs south of the Balcones escarpment in Texas.

Rhagoletis indifferens Curran

Rhagoletis cingulata, —Wilson and Lovett, 1913, Oregon Agr. Expt. Sta. Biennial Crop Pest and Hort. Rept., 1911–1912: 160 (first Northwest record of *cingulata*-like species). —Benjamin, 1934 (in part), U.S. Dept. Agr. Tech. Bull., 401: 9, 13, fig. 12, a-1 (synonymy of *indifferens* with *cingulata*). —Pickett, 1937 (in part), Canad. J. Res.

(D), 15: 53–75 (compares genitalic structure of *indifferens* with *cingulata*).
Rhagoletis indifferens Curran, 1932, Amer. Mus. Nov., 526: 6, 8 (on *Prunus emarginata* in Oregon). [Types examined: holotype ♂, Corvallis, Oregon, Aug. 17, 1931 (AMNH); allotype ♀ (same data as holotype); paratypes: Hood River, Oregon, 2 ♂ ♂, June 12, 1931; 1 ♂, June 23, 1931; 1 ♂, June 1931 (AMNH).][12] —Phillips, 1946, Mem. Amer. Ent. Soc., 12: 66–67, figs. 24, 69, 127, 171 (larval morphology, in key).
Rhagoletis cingulata indifferens Blanc and Keifer, 1955, Calif. Dept. Agr. Bull., 44: 77–88 (morphological differences between *indifferens* and *cingulata* discussed).

Diagnosis. With the exception of the characters cited below, *indifferens* fits the description of *cingulata*. It may be separated from all other species in the *cingulata* group by the presence of black shading on the posterior surface of coxa I. The epandrium is black instead of yellow as in the three eastern forms. A less useful character for separating *indifferens* from *cingulata* is the almost complete absence of an apical spot in *indifferens* (Table 8; Figs. 203–204). However, on rare occasions an apical spot may occur in *indifferens* (Fig. 205). Generally, *indifferens* is much more heavily pigmented with black than other species in the group. The thorax is always entirely black. The legs, although variable in color, are also more extensively shaded with black. The male abdomen (Fig. 51) lacks yellow shading on the apex of tergite V which is usually present in *cingulata*.

No significant differences in either the ejaculatory apodeme (Fig. 153) or any other structure of the male genitalia (Figs. 81, 107, 119) in sufficiently aged specimens were observed between this species and other members of the *cingulata* group. Such differences were reported by Curran (1932) in his original description of *indifferens*. Body and wing measurements are summarized in Tables 9A–9B; variation in ovipositor length is given in Figure 18.

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[12] Curran (1932) states that the type locality of both holotype and allotype is Hood River, Oregon. However, specimens bearing AMNH holotype and allotype labels in Curran's handwriting are from Corvallis, Oregon.

Geographical variation. There is no latitudinal color variation in this species as noted in *cingulata*. The southernmost populations from California are as heavily pigmented as those from British Columbia. There does seem to be a slight trend toward reduction in size in the California specimens, but this tendency is not as great as that noted in the related species, *cingulata*, and in some members of the *pomonella* and *suavis* groups.

Chromosome number and morphology (Fig. 225). The diploid number is 12; the MCA number is 22 as there are five pairs of metakinetic chromosomes and a single pair of acrokinetic dot chromosomes. No morphologically differentiated heterochromosomes (XY) or secondary constrictions were observed.

Source of cytological material: *P. emarginata*, Dunsmuir, California, Aug. 2, 1961; *P. avium*, Corvallis, Oregon, July 20, 1961, and vicinity of Mott Airport, Dunsmuir, California, Aug. 12, 1961. Cytological studies on larvae from *P. pennsylvanica* var. *demissa* were not made.

Courtship behavior. The courtship behavior of this species was not studied.

Parasites. Frick et al. (1954) have reared the following hymenopterous parasites from *indifferens*: *Opius ferrugineus* Gahan, *O. rosicola* Muesebeck, *Opius* sp. (Braconidae); *Phygadeuon epochrae* Viereck (Ichneumonidae); *Trybliographa* sp. (Cynipidae); *Tetrastichus faustus* Burks (Eulophidae); *Pachycrepoideus dubius* Ashmead; *Halticoptera* n. sp., *Eupteromalis* sp. near *americanus* Gahan (Pteromalidae); *Psilus* sp. (Diapriidae). Two of these species, *T. faustus* and *P. dubius*, are also parasites of *R. fausta*.

Hosts. The host relationships of *indifferens* have been presented in detail by Frick et al. (1954); therefore only a brief summary will be given here with the addition of references appearing since 1954.

The first report of *indifferens* in cultivated cherries (*P. avium* L.) growing in Oregon was made by Wilson and Lovett

(1913) about 89 years after the introduction of the first cherry seedlings into the Northwest (Jones, 1963, *in litt.*). The native host of this species, *Prunus emarginata* (Dougl.) D. Dietr. (wild pin cherry), was first reported by Keifer (1938), and later Frick et al. (1954) added P. *virginiana* L. var. *demissa* (Nutt.) Torr. to the host list. Recently two more *Prunus* species have been found to be hosts of the western cherry fruit fly. Ellertson (1961) reported larvae of *indifferens* infesting the fruits of *P. subcordata* Benth (Pacific plum) near The Dalles in Oregon, and the introduced *P. salicina* Lindl. (Japanese plum) at Hood River, Oregon. This is the first record of a member of the *cingulata* group infesting plums.

Distribution (Map 5). *R. indifferens* does not reach as far south or as far north as its principal host, *P. emarginata*. Its presence in Montana beyond the range of this wild cherry represents recent introduction of *indifferens* into commercial cherry growing areas.

Rhagoletis osmanthi new species

Types. Holotype ♂, Osceola Co., Florida, larva collected Nov. 13, 1929, emerged Oct. 18, 1930, ex *Osmanthus americanus* (Slight) (USNM, No. 67376); paratypes: 3 ♂ ♂ 5 ♀ ♀, Alligator Lake, Osceola Co., fruit collected Nov. 13, 1929, ex *O. americanus* (Slight) (USNM).

This species and the one following are being described from material reared during the 1929–1933 Mediterranean fruit fly campaign in Florida where extensive collections of native fruit flies were made on a wide variety of host plants. The taxonomic results of these investigations were summarized in a publication by Benjamin (1934), and the biology in an unpublished but extremely useful report by Nicholson (1929–30).

Benjamin noted that specimens reared from cultivated cherries (probably from the Northeast as cultivated cherries are not grown in Florida) and material from

MAP 5

- ●   RHAGOLETIS CINGULATA
- ◉   RHAGOLETIS INDIFFERENS
- ——   PRUNUS SEROTINA
- —·—·—   PRUNUS VIRGINIANA (ARROW)
- ·············   PRUNUS EMARGINATA

SCALE

MILES

LAMBERT'S AZIM THALES A AREA PROJECTION

Florida associated with the fruits of wild tea-olive and fringe trees (Oleaceae) were larger than those reared from native Florida wild cherry, *Prunus serotina*. He did not consider these differences worthy of further recognition. It is evident, however, that the populations associated with wild olives in Florida represent two very closely related sibling species.

Diagnosis. R. *osmanthi* can be distinguished from *cingulata* in Florida by the following combination of characters: (1) the presence of a forked apical wing band; (2) a longer ovipositor (for comparison with *cingulata*, see Fig. 18); (3) considerably larger size (Tables 9A–9B); (4) *osmanthi* infests only the fruits of *Osmanthus* spp.

It is more difficult to differentiate *osmanthi* from the other olive infesting species, *chionanthi*, as both have a forked apical wing band. The latter species is distinctly smaller than *osmanthi* (Tables 9A–9B; Fig. 18), although some overlap in both sexes does occur. Rearing records also indicate that these fly populations are allochronically isolated with their emergence synchronized with the maturation of their respective host fruits (see *Hosts*). Adults of R. *osmanthi* occur in the winter months between October and January, while *chionanthi* is active only in the summer from mid-July to early August.

The only useful character for separating these species is the difference in ovipositor length. But even this may not be reliable when host data is lacking and only one specimen is being considered as it may fall within the range of *chionanthi*. On a population basis, however, the ovipositor length between these two species is significantly different at the .05 level using the standard t-test ($t_{18,\ .05} = 2.10 < 4.07 \therefore$ reject Ho). Thorax length may be used to distinguish males (see Table 9A), although the variation in this character is somewhat higher than ovipositor length.

In all other respects *osmanthi* fits the description of *cingulata*. Figures of the wing (206), abdomen (53–54), and male genitalia (82, 108, 120, 155) are included for comparative purposes. Body and wing measurements may be found in Tables 9A–9B.
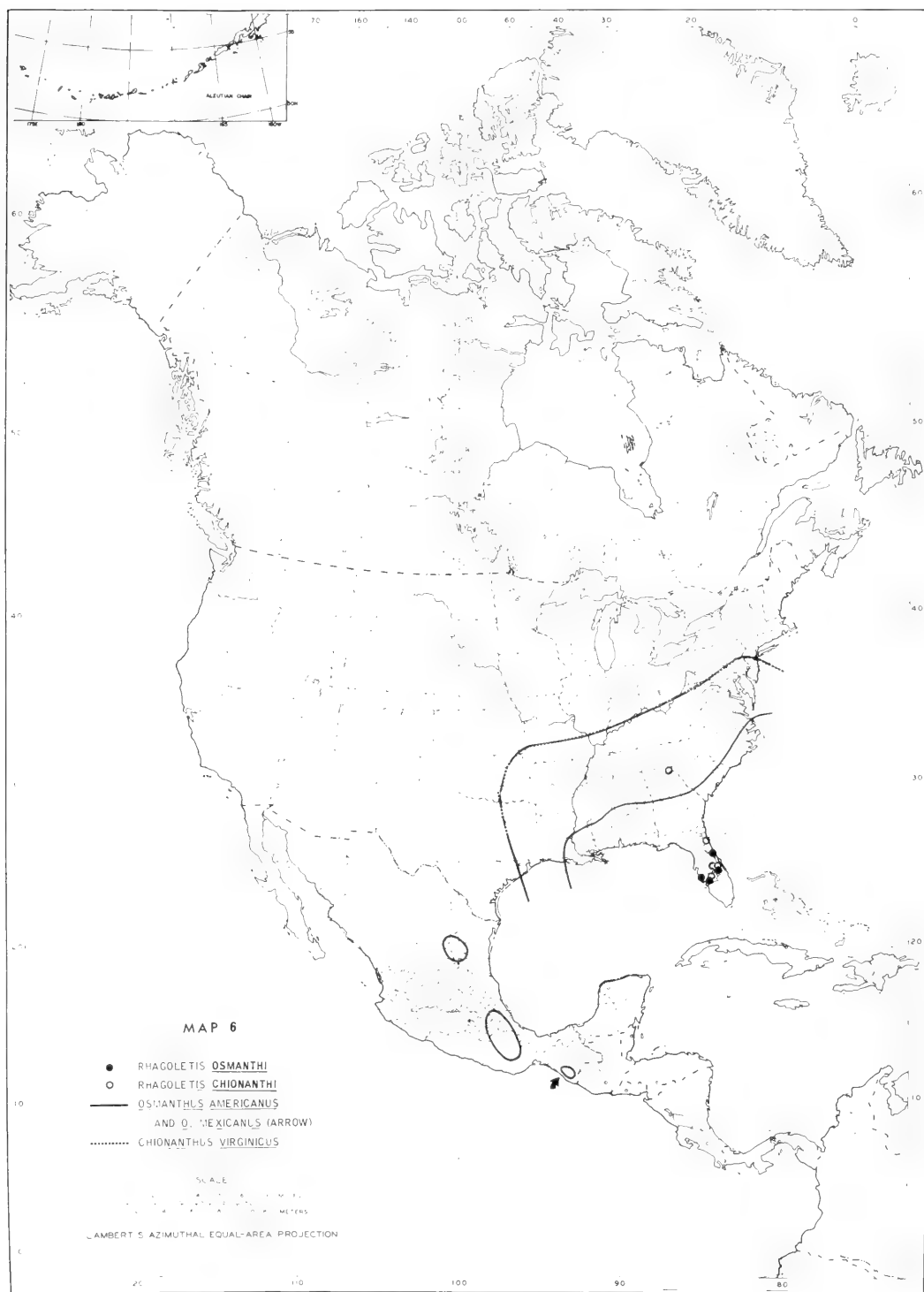
It should be stressed that *osmanthi*, as well as the closely related *chionanthi*, is much more extensively marked with yellow than the northeastern population of *cingulata*. However, it is impossible to differentiate between the Florida representatives of *cingulata*, *osmanthi*, and *chionanthi* as they have similar color patterns.

There is never a trace of black or dark brown maculation on the postcranial regions or on any segments of the legs in *osmanthi*, and there are also extensive areas of yellow on the pleural regions and on the tergites of the abdomen.

Chromosome number and morphology. The chromosomes of this species have not been studied.

Hosts. R. *osmanthi* has been reared only from *Osmanthus americanus* (L.) Gray (wild tea-olive, devilwood) growing in Florida. *Osmanthus* (Oleaceae) is a genus of more than 30 species primarily of eastern and northeastern Asia with only two to four species represented in North America (Wilson and Wood, 1959). At least three allopatric variants have been described from peninsular Florida, some of which are recognized as distinct species. It is not known if R. *osmanthi* infests all these forms, but considering the oligophagous nature in host specificity recorded for other *Rhagoletis* species, it is reasonable to assume that it does.

O. americanus occurs from central Florida north along the coastal plain to southeastern Virginia, and west to southeastern Louisiana (see Map 6). Isolated populations of this species also occur in Nuevo Leon, Oaxaca, and Vera Cruz, Mexico, with a second species, *O. mexicanus* Lundell, known from a single locality in Chiapas, Mexico (Green, 1958; Wilson and Wood, 1959). R. *osmanthi* may therefore cover a wider range than its present Florida

MAP 6

•   RHAGOLETIS OSMANTHI
○   RHAGOLETIS CHIONANTHI
――― OSMANTHUS AMERICANUS
     AND O. MEXICANUS (ARROW)
····· CHIONANTHUS VIRGINICUS

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records indicate. Collection and rearing data suggest that *osmanthi* is common on its host fruit from October through January. Nicholson (1929–30) reports that flies emerge following a nine- to eleven-month diapause from mid-September to mid-March. This emergence closely corresponds to the maturation time of the host fruit and as yet is not known to overlap the emergence periods of the closely related species *chionanthi* (mid-July to early August).

Distribution (Map 6). The species has been recorded in the following Florida localities: De Leon Springs, Coronado Beach, Volusia Co.; Alligator Lake and 7 mi. E Kissimmee, Osceola Co.; Seffner, Thonotosassa, Hillsborough Co.; Tarpon Springs, Pinellas Co.; New Port Richey, Pasco Co.

Rhagoletis chionanthi new species

Types. Holotype ♀, Apopka, Florida, larva collected Sept. 12, 1929, emerged June 13, 1930, ex *Chionanthus virginicus* (W. S. Earle) (USNM No. 67377); paratypes: 3 ♂ ♂ 6 ♀ ♀, 6 mi. SW Kissimmee, Florida, July 1930, ex *C. virginicus* (G. F. Harding) (USNM).

Diagnosis. The characters separating *chionanthi* from the closely related species *osmanthi* are (1) a mean difference in ovipositor length (Fig. 18), and (2) a difference in host preference and emergence period. The emergence is synchronized to coincide with the ripening of the fruits of *C. virginicus*. No entirely suitable method has been found to separate the males of the two olive infesting species, although thorax length may tentatively serve to identify some specimens. For a detailed discussion of the differences between these two species, see the diagnosis of *osmanthi*.

In all other respects *chionanthi* fits the description of *cingulata*. Figures of the wing (207), abdomen (55–56), and male genitalia (80, 109, 121, 154) are included for comparative purposes. Body and wing measurements may be found in Tables 9A–

9B. For the variation in ovipositor length consult Figure 18.

As in the case of *osmanthi*, *chionanthi* can be easily distinguished from north-eastern representatives of *cingulata* on the basis of color pattern. The similarities between these three species in Florida make it impossible to separate them on the basis of color alone.

Chromosome number and morphology. A cytological study of this species was not made.

Hosts. Nicholson (1929–30) reared this species from *Chionanthus virginicus* L. (fringe-tree or old man's beard) (Oleaceae). This small genus of plants is represented by three or four species, two in eastern North America and one or two in eastern Asia. *C. virginicus* ranges from Florida to Texas northward to New Jersey, Pennsylvania, West Virginia, southern Ohio, southern Missouri, and Oklahoma (see Map 6). A second species, *C. pygmaeus* Small is endemic of the sandscrub of the lake region of central Florida (Wilson and Wood, 1959) and may also be infested by *chionanthi*. As in the closely related species, *R. osmanthi*, *chionanthi* probably has a much wider distribution than indicated by the specimens available for study.

Nicholson reports that this species is active from mid-July to early August.

Distribution (Map 6). *R. chionanthi* has been recorded from Satalah, Rabun Co., Georgia, and the following Florida localities: Apopka and Wakiwa Springs, Orange Co.; vicinity of Kissimmee, Osceola Co.; St. Augustine, St. Johns Co.; Lake Juliana, Auburndale, Polk Co.

SUAVIS SPECIES GROUP[13]

The members of the *suavis* group are of particular interest in that they provide a completely different picture of speciation from that of the *pomonella* and *cingulata*

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[13] Benjamin (1934) referred to this complex as the *juglandis* group. I have chosen to follow Cresson (1929) who originally established the group to include all the walnut infesting species.

groups. The predominance of allotrophic sibling species is the outstanding feature of the latter two groups where a wide range of host families and genera have been adopted in the course of speciation. These drastic shifts in hosts have been accompanied by only slight morphological changes. Members of the *suavis* group, on the other hand, are syntrophic as they are capable of infesting only species within the genus *Juglans* (Juglandaceae) (Boyce, 1934; Christenson and Foote, 1960). Unlike the *pomonella* and *cingulata* complexes, the walnut infesting species have developed a wide range of morphological differences, particularly in size and body coloration. These differences are so distinct that it is possible to recognize each species without microscopic examination.

Diagnosis. The *suavis* species group may be distinguished from others in the genus *Rhagoletis* by the following combination of characters: (1) males have a well developed pouch-like invagination located in the membrane between the genital ring and fultella (Fig. 75, GRMP); (2) the scutellum is concolorous cream to light yellowish orange without a distinct spot as in most other *Rhagoletis* species; (3) the setae and microtrichia covering the dorsum do not form a pattern of vertical stripes but present a homogeneous appearance; (4) the larvae normally feed in the husks of various *Juglans* species.

Sexual dimorphism in color patterns of the thorax and abdomen are present in *completa, zoqui,* and to a lesser extent, *suavis.* Males of *completa* and *zoqui* have more extensive black markings on the legs, pleural regions of the thorax, and abdominal tergites than do the females. The variation in color pattern between the sexes of *suavis* is limited to the abdominal tergites. The degree of coloration in the three species varies considerably among individuals with some heavily colored females approaching the color of lightly pigmented males.

The chromosome number (n=12) and morphology are identical in all species, with five metakinetic and two small acrokinetic dot chromosomes. No heteromorphic sex chromosomes were noted.

Rhagoletis suavis (Loew)

Trypeta suavis Loew, 1862, Smithson. Misc. Coll., 6: 63, 75, pl. 2, fig. 10. [Type examined: sex unknown (only wings and part of dorsum remain of this specimen), "Middle States" (MCZ, No. 13293).]
Acida suavis, —Osten Sacken, 1878, Smithson. Misc. Coll., 16: 189 (notes type in MCZ).
Rhagoletis suavis, —Coquillett, 1899, J. New York Ent. Soc., 7: 260 (new status). —Bezzi, 1911, Boll. Lab. Zool. Portici, 5: 7, 14 (description, in key, hosts). —Phillips, 1923, J. New York Ent. Soc., 31: 135–136, pl. 18, fig. 24 (in key, host). —Cresson, 1929, Trans. Amer. Ent. Soc., 55: 411–412 (in key, redescription). —Boyce, 1934, Hilgardia, 8: 375–376, figs. 4, 12, 13 (biology, description, interspecific relationships). —Pickett, 1937, Canad. J. Res. (D), 15: 61, fig. 11 (genitalia, compared with *completa*). —Phillips, 1946, Mem. Amer. Ent. Soc., 12: 26, 74–76, figs. 30, 75, 136, 137, 177 (larval description, in key).

Diagnosis. The wing pattern of *suavis* may be used to separate this species from its closest relative, *completa.* The medial and subapical bands in *suavis* are normally joined by a broad fuscous band extending diagonally across M_{1+2} between r-m and m (Fig. 190). In some specimens this band may be broadened to cover most of the region in the discal cell between r-m and m (Fig. 191). Specimens of *completa* may have the medial and subapical crossbands joined by a narrow fuscous bridge at right angles to the two crossbands at various points in the regions of cell 1st M_2 (discal cell), as illustrated in Figure 193, and by Foote and Blanc (1963, Fig. 73). This pattern is readily distinguished from that of *R. suavis* in that it is never diagonal to the long axis of the wing. The medial band is also much wider in *suavis* than in *completa.* The presence of a concolorous yellow postscutellum in both sexes of *suavis* may also be used to distinguish this species from *completa* which has this region either marked by two broad vertical brown bands or is concolorous brown.

In a study of the genitalia of these two species, Pickett (1937) found no distinct differences in the tip of the aedeagus or in the surstyli. He thus concluded that the genitalia are of no use in distinguishing between *suavis* and *completa*. However, I have found that the genitalia do offer the following useful characters. The tip of the aedeagus in *suavis* bears a setulose finger-like appendage (Fig. 129), while in *completa* the tip is modified to form a rake-like fluted appendage (Fig. 131). Also, the vesica of the latter species is bifurcate, while in *suavis* it is entire. Boyce (1934) noted that the surstyli of *completa* when viewed mesolaterally are somewhat curved and taper gradually from the region of the prensisetae toward the distal end, while those of *suavis* are only very slightly curved and taper abruptly at the distal end. Pickett (1937) correctly pointed out that in order to get the surstyli to appear like those in Boyce's figure, it is necessary to orient the epandrium so that a posterior lateral view is obtained. Nevertheless, there are slight but consistent differences between the surstyli of the two species, although not as obvious as figured by Boyce. The surstyli of *suavis* are slightly thicker in the region of the prensisetae and therefore less curved in appearance than those of *completa* (Figs. 73, 75). The structure of the ejaculatory apodeme was also used by Boyce to separate these two species, but as already pointed out by both Pickett (1937) and myself, this structure is of little use in differentiating most members of the genus *Rhagoletis*.

Description. Body and wing measurements in Tables 10A–10B. *Head* (Fig. 30): mentum, postcranial, postgenal, and gular regions golden yellow with postorbital region light golden yellow to cream; frontalia, parafrontalia, parafacialia and genae yellowish orange; face tannish cream. Occipital, postvertical (0-2), postorbital (7-15), genal, and well developed gular bristles golden yellow to yellowish orange; all other major bristles black. No black or brown markings on head. *Thorax*: dorsum golden yellow, covered evenly with decumbent golden yellow setae and silvery white to golden yellow pollinose microtrichia. Dorsocentrals slightly behind anterior supraalars. Pleural and sternopleural regions golden yellow without distinct black markings in either male or female. Propleural bristles light yellow; two mesopleural bristles of about equal size. Notopleural stripe cream to white; dorsum of scutellum cream at apex, grading to golden yellow at base. Postscutellum and halteres concolorous golden yellow. *Legs*: all segments golden yellow. Dorsal rows of erect to semierect long bristles in femur I golden yellow, postventral row black. A row of semierect golden yellow short bristles along anterior surface of tibia II, well differentiated from shorter decumbent setae. Tibia III with row of weakly differentiated stout semierect golden yellow setae on anterior outer surface. *Wing*: Normal wing pattern as in Figure 190, with Figure 191 representing an extreme in variation of pattern. In all specimens thus far examined medial band always joined to subapical band by a diagonal fuscous band crossing M_{1+2} between crossveins r-m and m. Some individuals may have fuscous area joining these two bands broadened, reaching from M_{1+2} almost to posterior margin of wing. Medial band not joined to basal band and ending in cell Cu_1. *Abdomen*: base color of all tergites golden yellow to dark yellowish orange; tergites I–III of male (Fig. 59) and I–IV of female (Fig. 60) bearing pollinose cream colored band along posterior margin; tergites of male usually progressively more heavily shaded with black markings from basal segments to apex. *Genitalia: male*—epandrium (Figs. 75, 99) yellowish orange to dark brown with surstyli yellowish orange to golden yellow; aedeagus (Fig. 129) with finger-like appendage covered with short setae at tip, resembling that of *juglandis* (Fig. 130); vesica smooth, unforked; genital ring pouch well developed (Fig. 75, GRMP); phallic apodeme

	R. ...	R. ...pet	R. ...glandis	R.	R. ...di
n	17	14	10	10	10
HL	1.06±.036	1.06±.030	.91±.031	.97±.045	1.17±.026
	(.81-1.30)	(.88-1.23)	(.79-1.06)	(.79-1.32)	(1.08-1.30)
HW	1.63±.051	1.59±.046	1.37±.041	1.39±.064	1.76±.041
	(1.34-1.90)	(1.31-1.81)	(1.22-1.53)	(1.14-1.79)	(1.58-1.94)
HH	1.41±.037	1.33±.040	1.11±.037	1.17±.052	1.52±.044
	(1.12-1.61)	(1.11-1.51)	(.96-1.28)	(1.00-1.55)	(1.31-1.70)
FW	.82±.018	.80±.020	.71±.025	.68±.032	.88±.016
	(.73±.91)	(.69-.91)	(.60-.80)	(.56-.88)	(.82-.95)
LH	1.13±.028	1.09±.034	.91±.032	.97±.048	1.24±.028
	(.88-1.29)	(.88-1.26)	(.76-1.04)	(.80-1.29)	(1.13-1.38)
F:W	.59±.018	.54±.018	.51±.016	.50±.021	.55±.017
	(.48-.71)	(.41-.62)	(.44-.58)	(.40-.61)	(.47-.62)
*L	.53±.011	.53±.016	.43±.011	.48±.023	.60±.012
	(.44-.60)	(.44-.60)	(.39-.49)	(.39-.60)	(.55-.65)
FL	.7 ±.0	.78±.026	.67±.025	.68±.041	.88±.024
	(.55-.95)	(.63-.92)	(.57-.80)	(.55-.95)	(.79-1.00)
GW	.28±.021	.26±.011	.21±.001	.20±.013	.28±.013
	(.21-.36)	(.20-.32)	(.17-.24)	(.16-.30)	(.21-.35)
!!	2.60±.045	2 24±.071	1.85±.064	2.13±.070	2.72±.068
	(2.14-3.08)	(1.77-2.59)	(1.57-2.10)	(1.66-2.97)	(2.41-3.06)
.	15	18	10	10	10
WL	4.57±.099	3.76±.104	3.41±.129	4.30±.171	4.71±.161
	(3.83-4.97)	(2.75-4.32)	(2.94-3.99)	(3.53-5.30)	(3.99-5.53)
WW	2.22±.049	1.90±.060	1.62±.064	1.95±.078	2.29±.074
	(1.86-2.45)	(1.31-2.29)	(1.41-1.96)	(1.60-2.45)	(1.93-2.61)

Table 10A. Body and wing measurements of males of the
suavis species group. Figures represent mean, standard
error, and range.

	R. s....	R.	R. ...g...	R.	R. ....
.	.	14	.,	1.	.
HL	1.09±.026	1.06±.038	.94±.031	.96±.024	1.17±.019
	(.85-1.21)	(.71-1.21)	(.83-1.04)	(.84-1.08)	(1.06-1.24)
HW	1.65±.031	1.56±.045	1.41±.047	1.42±.048	1.79±.027
	(1.38-1.82)	(1.17-1.78)	(1.20-1.63)	(1.22-1.54)	(1.62-1.90)
HH	1.31±.010	1.29±.043	1.15±.043	1.18±.031	1.52±.025
	(1.18-1.57)	(.92-1.44)	(.95-1.34)	(1.00-1.31)	(1.37-1.63)
FW	.82±.015	.79±.026	.71±.022	.71±.017	.90±.001
	(.70-.89)	(.54-.92)	(.60-.78)	(.62-.78)	(.84-.95)
FH	1.13±.026	1.07±.029	.92±.032	.98±.026	1.27±.022
	(.95-1.28)	(.72-1.21)	(.80-1.07)	(.85-1.08)	(1.13-1.35)
F:W	.59±.019	.54±.020	.55±.026	.48±.018	.52±.001
	(.45-.63)	(.37-.65)	(.41-.68)	(.36-.55)	(.46-.56)
*L	.54±.012	.51±.018	.44±.014	.49±.011	.61±.011
	(.46-.62)	(.35-.60)	(.38-.52)	(.43-.54)	(.54-.66)
FL	.79±.020	.77±.030	.70±.026	.69±.018	.87±.017
	(.64-.87)	(.49-.90)	(.57-.81)	(.59-.75)	(.75-.95)
GW	.28±.016	.26±.013	.23±.013	.20±.007	.28±.001
	(.18-.34)	(.16-.32)	(.17-.30)	(.15-.22)	(.22-.31)
IL	2.54±.071	2.22±.009	1.94±.077	2.13±.072	2.71±.045
	(2.06-2.86)	(1.43-2.63)	(1.57-2.30)	(1.73-2.56)	(2.52-2.95)
:	15	18	10	10	10
WL	4.57±.122	3.75±.095	3.70±.098	4.30±.050	4.91±.088
	(3.86-5.36)	(3.11-4.28)	(3.24-4.12)	(3.73-4.68)	(4.45-5.36)
WW	2.25±.060	1.91±.052	1.70±.092	2.00±.046	2.46±.035
	(1.86-2.55)	(1.50-2.19)	(1.54-2.03)	(1.77-2.26)	(2.29-2.68)

Table 10B. Body and wing measurements of females of the
suavis species group. Figures represent mean, standard
error, and range.

straight or only slightly bent. Ejaculatory apodeme normal (Fig. 141). *Female*—variation in ovipositor length (Fig. 20); ovipositor sheath yellowish orange to chestnut brown; three cylindrical spermathecae with very small appressed scale-like papillae (Fig. 157); ovipositor tip with two pairs minute preapical setae.

Geographical variation. There is no evidence of geographical variation in the morphology or in wing and body color patterns of this species. Adult size seems to vary considerably within a given region, a feature common to all members of this species group. The apparent reason for this size variation may be mainly a nutritional one. Crowding occurs frequently as females oviposit readily in the same walnut (Boyce, 1934); the husk may therefore be consumed before the larvae are fully mature. In the material examined there was no apparent tendency for the adults to become progressively smaller toward the southern distributional limits, a characteristic of the related species, *completa*, and certain members of other species groups (i.e., *cingulata* and *pomonella*).

Chromosome number and morphology (Figs. 218–219). The diploid number is 12; the MCA number is 22 as there are five pairs of metakinetic chromosomes and a single pair of acrokinetic dot chromosomes. No morphologically differentiated heterochromosomes (XY) or secondary constrictions were observed.

Source of cytological material: *Juglans cinerea*, Cambridge, Mass., 8 Sept. 1960; *J. nigra*, Pemberton, New Jersey, 15 Oct. 1961.

Courtship behavior. Courtship has been described by Brooks (1921) and is similar to that reported for *completa* by Boyce (1934).

Single males set up and defend temporary territories on nuts suitable for oviposition. Walnuts are preferred which show some mechanical damage to the husk in which the female can readily 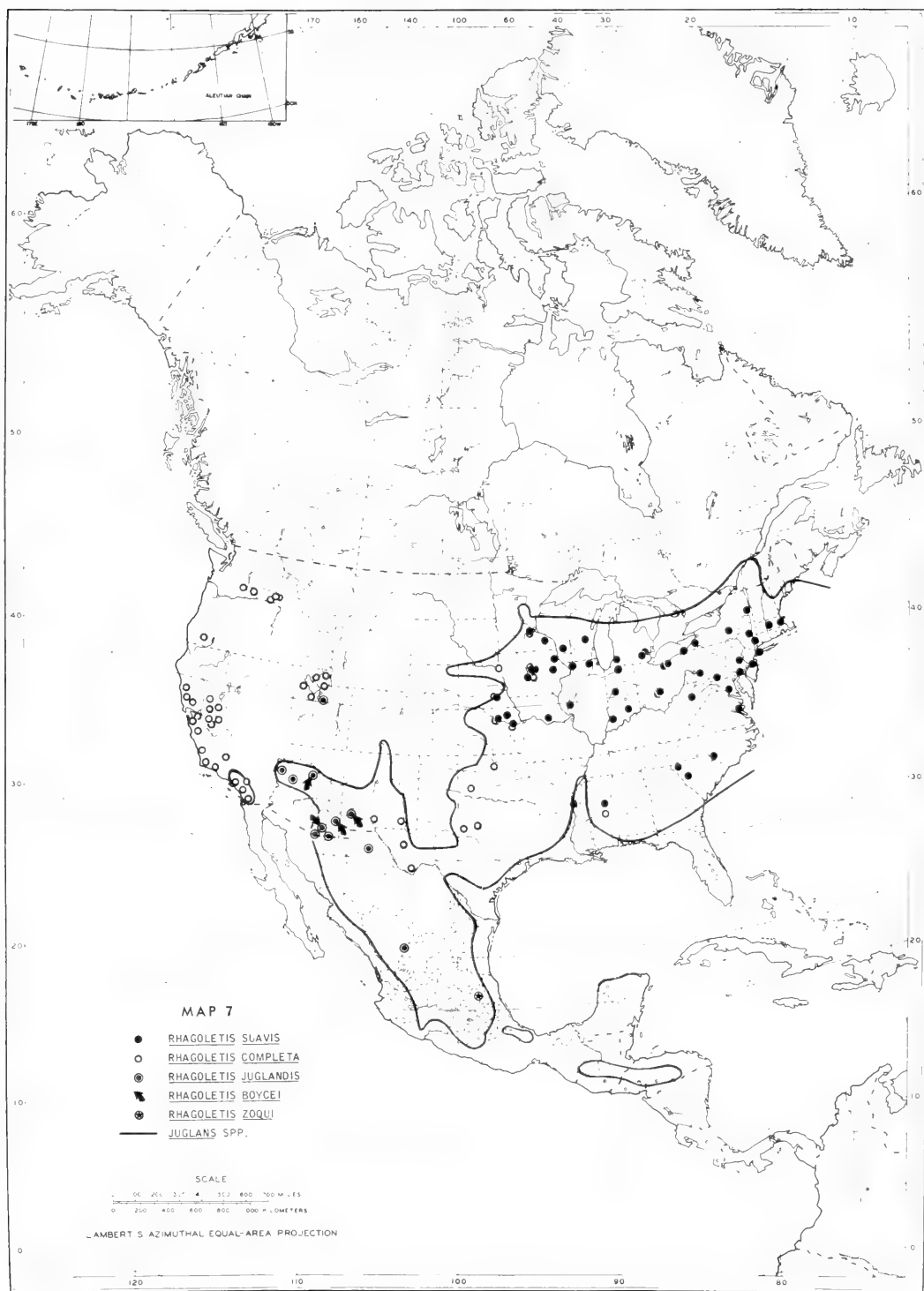oviposit. The males remain for hours on this site where they patrol in short turning movements about the nut. When another male alights on the nut, the original occupant attacks with lunging movements, the wings at first held vertically above the thorax followed by wing waving. If the resident male fails to dislodge the new arrival, the pair will enter into a "boxing match," both reared on their hind legs, striking and grappling with their fore legs. Usually the original occupant succeeds in driving off the other male or both fall off the nut and only one (presumably the resident male) returns, whereupon he begins once again to patrol the nut.

Brooks described the approach of the female as slow and deliberate, taken in stages of flying and crawling on leaves and twigs near the nut before alighting on it. When the male observes the approaching female, he becomes excited and rapidly moves back and forth, whirling around and raising and lowering his wings with the white spot and dark body in sharp contrast to the green walnut husk.

On the arrival of the female, the male backs away from the oviposition site and remains stationary with wings elevated above the back while facing the female. When the female attempts to oviposit, the male usually springs upon her and copulation takes place. This is often followed by alternate periods (4–5) of egg laying and copulation, the male sometimes remaining mounted and sometimes dismounting. After the female has left, the male frequently remains on guard and resumes his patrolling.

There appears to be a strong tendency for flies to congregate only in certain trees and on the lower branches. Feeding on the exudates emanating from oviposition sites has been observed many times.

Parasites. Babb (1902) reared *Aphaereta auripes* Provancher (Hymenoptera, Alysiidae) from larvae collected at Amherst, Mass. No other parasites have been described from this species, nor have I been

MAP 7

- ● RHAGOLETIS SUAVIS
- ○ RHAGOLETIS COMPLETA
- ◉ RHAGOLETIS JUGLANDIS
- ✦ RHAGOLETIS BOYCEI
- ✺ RHAGOLETIS ZOQUI
- — JUGLANS SPP.

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able to rear parasites from walnuts collected at five widely separated localities.

Hosts. This species has been reared only from the husks of *Juglans* species. A single report by Stirrett (1936) that *suavis* occurs also in hickory nuts (*Carya*, Juglandaceae) should be accepted with some caution. No *Rhagoletis* has actually been reared from *Carya* by any investigator. Stirrett merely states that local growers of commercial walnuts had reported *suavis* mining in the husks of local hickory nuts, but he did not confirm this observation through rearing. It is sometimes easy for the untrained observer to confuse a fly maggot with a lepidopterous larva, as Biederman probably did when he described the larva of *juglandis* descending from a walnut to the ground on a thread (Cresson, 1920).

Larvae of *suavis* have been reared from the following host plants: *Juglans nigra* L. (black walnut) (Babb, 1902, and others); *J. cinerea* L. (butternut) (Banks, 1912, and others); *J. regia* L. (Persian or English walnut, native to western Europe and Asia) (Brooks, 1921, and others); *J. Sieboldiana* Maxim. (native to Japan) (Brooks, 1921).

Distribution. As illustrated in Map 7, *suavis* covers the eastern two-thirds of the range of *J. nigra* and probably the entire range of *J. cinerea*. Records of *suavis* from Oklahoma and Texas are lacking and in these regions *completa* seems to be the only species on *J. nigra*.

Rhagoletis completa Cresson

Rhagoletis suavis completa Cresson, 1929, Trans. Amer. Ent. Soc., 55: 412, pl. 16, fig. 9. [Type examined: ♂, Chino, San Bernardino Co., Calif., Aug. 10, 1928, Persian walnut (A. M. Boyce) (ANSP, No. 6364); paratypes examined: 2 ♀ ♀, same data as type; 1 ♀, Chino, Calif., Aug. 15, 1929 (A. M. Boyce) (ANSP, No. 6341; MCZ, No. 19467); 1 ♀, Pomona, Los Angeles Co., Calif., Aug. 10, 1929 (A. M. Boyce) (ANSP, No. 6364).] —Pickett, 1937, Canad. J. Res. (D), 15: 61 (genitalia, status).

Rhagoletis completa, —Boyce, 1931, J. Econ. Ent., 24: 1018–1024 (diapause). —Curran, 1932, Amer. Mus. Nov., 526: 6. —Boyce, 1934, Hilgardia, 8: 361–579 (bionomics, control).

—Phillips, 1946, Mem. Amer. Ent. Soc., 12: 27, 64–65, figs. 31, 76, 138, 139, 178 (larval morphology, in key).

Diagnosis. In general appearance similar to *suavis*, but smaller and displaying more marked sexual dimorphism in body coloration. The differences in the wing pattern, body markings, and aedeagal morphology make it easy to differentiate this species from *suavis*, its closest relative. For a discussion of these differences, see the diagnosis of *suavis*.

Description. Body and wing measurements in Tables 10A–10B. Male and female about same size. *Head* (Fig. 28): entirely yellow. Postcranial region light yellowish orange; postorbital region light yellow; frontalia golden yellow, parafrontalia slightly lighter; parafacialia light yellow, in distinct contrast with golden yellow face; genae light yellowish orange grading to white posteriorly; postgenal regions and gulamentum white with faint tint of yellow; mentum light brown. Genal, occipital, postvertical, postorbital (7–12), and strong gular bristles yellow to yellowish orange; all other major bristles black. *Thorax: male*—dorsum concolorous tawny to raw sienna, uniformly covered with light yellow to golden yellow decumbent setae and microtrichia, without vertical banded pattern. Propleural bristles light yellow; all other major bristles black. Two mesopleural bristles of about equal size. Pleural and sternopleural regions brownish black. Notopleural stripe light yellow; scutellum light yellow grading to deeper golden yellow at base; halteres golden yellow. Base color of postscutellum golden yellow with two broad vertical brownish black bands; some specimens with postscutellum concolorous brownish black. *Female*—dorsum, humeral stripe, and scutellum as in male. Pleural and sternopleural regions lighter with variable brownish black markings on pleural regions, rarely slight brownish black markings on dorsal margin of sternopleuron. Vertical stripes present on postscutellum but frequently much narrower than in

male. *Legs: male*—coloration highly variable. Coxae I and II generally brownish black; coxa III golden yellow. Trochanters golden yellow to tan. Femur I brownish black with dorsal rows of bristles golden yellow to brownish black; ventral row black. Femur II tan with single row of weak semierect stout setae on anterior surface. Femur III golden yellow or tan grading to brownish black ventrally. Fifth and occasionally part of fourth tarsal segment on each leg dark brownish yellow, remaining segments tan to golden yellow. Tibiae I and II straw colored. Tibia III golden yellow grading to brownish black ventrally; outer surface with single row of about eight yellowish orange semierect setae. *Female*—all leg segments golden yellow without black markings; last tarsal segment sometimes dark yellowish brown. All setae and bristles as in male. *Wing* (Figs. 192–193): pattern convergent with that of *R. berberis* (Fig. 202) to which *completa* apparently bears no close relationship. Medial band rarely joined to subapical band; if joined then only narrow fuscated bridge at right angles to two crossbands present and never angled as in *suavis* (Fig. 190); medial band not joined to basal band. Junction of R_{2+3} and R_{4+5} with 0 to 2 setae dorsally, 0 to 2 ventrally; R_{4+5} bare. Anal cell strongly pointed with r-m about midway between crossveins M_3 and m. *Abdomen: male* (Fig. 63)—coloration highly variable. Normally tergites I and II golden yellow with some brownish black shading on either side of medial line. Tergites III–V generally golden yellow but becoming progressively more heavily marked with brownish black; tergite V usually almost entirely brownish black. Tergites II, III, and IV with pollinose cream colored band along posterior margin. *Female* (Fig. 64)—as in male, coloration variable, but all segments substantially more golden yellow than male. Tergites III–V usually marked with some dark shading on either side of medial line and with cream colored pollinose band along posterior margin of tergites III–VI.

Genitalia: male—epandrium and surstyli golden yellow (Figs. 73, 97), surstyli somewhat narrower than those of *suavis* (Figs. 75, 100); aedeagus with fluted, rake-shaped apical appendage (Fig. 131); genital ring pouch well developed; phallic apodeme straight. Ejaculatory apodeme normal (Fig. 145). *Female*—variation in ovipositor length shown in Figure 20; ovipositor sheath golden yellow to brown; three cylindrical spermathecae with very small appressed, scale-like papillae (Fig. 158), similar to those found in *suavis* except narrower (Fig. 157); ovipositor with two pairs of minute preapical setae.

Geographical variation. There is a marked trend toward reduction in size in specimens from the Southwest (Texas and New Mexico). Not enough material was available for a statistical analysis. This tendency has also been noted in *pomonella* and *cingulata*, and apparently is correlated with a shift to a more arid habitat. A series of specimens from Lincoln, Nebraska, are also considerably smaller than those from the neighboring states of Minnesota, Iowa, and Kansas (see Fig. 20 for comparison of ovipositor length). These specimens are all teneral indicating that they were probably reared and killed before they had attained full coloration. The reason for their small size is not known, but they may have emerged from overcrowded conditions as they all resulted from a single collection of walnuts.

Chromosome number and morphology (Fig. 220). The diploid number is 12; the MCA number is 22 as there are five pairs of metakinetic chromosomes and a single pair of acrokinetic dot chromosomes. No morphologically differentiated heterochromosomes (XY) or secondary constrictions were observed.

Source of cytological material: *J. regia*, Anaheim, California, 15 Aug. 1961; *J. californica*, Riverside, California, 15 Aug. 1961.

Courtship behavior. The courtship behavior of *completa* is similar to that of *suavis* and has been briefly outlined by

Boyce (1934). Males are territorial and usually begin patrolling walnuts in the late afternoon when mating is most frequently observed. Resident males recognize and attack any male or other insect that lands on the walnut. In aggressive display, the wings are held vertically above the thorax. This display is used in the preliminaries of courtship by *suavis*. The resident male attempts to repel the intruder by rushing and butting. If this fails to dislodge the intruder, then a "boxing match" may follow, with both flies standing on their hind legs venter to venter, striking each other with the fore and middle legs. Aggressive displays and fighting may last as long as two to three minutes before one of the males flies away.

The male reacts very differently to the female when she lands on the walnut. His movements become more rapid and excited. Facing the female and moving sideways, he attempts to circle her; she will either ignore the male and begin ovipositing or fly away. As soon as oviposition is completed, the male mounts. In *suavis*, mating may occur before oviposition. As the male mounts, the female spreads her wings laterally, raises her abdomen and extrudes the ovipositor which the male grasps with the surstyli. Mating in the field lasts from two to fifteen minutes.

Parasites. Two apparently general-feeding parasites of dipterous pupae have been reared from *completa*. These are *Spalangia rugosicollis* Ashmead (Chalcididae), and *Salesus* sp. (Proctotrypoidea) very near *atricornis* Ashmead (Boyce, 1934). Boyce also reports that a larval parasite, *Opius humilis* Silvestri (Braconidae), introduced from Hawaii was successfully established in California on *R. completa*.

Hosts. *R. completa* has been reared from *Juglans nigra*, a species which is native to eastern North America but falls within the normal range of *completa* in Minnesota, Iowa, and the eastern part of Kansas, Oklahoma, and Texas (Boyce, 1934, and others). Soon after the introduction of *completa*

into California, sometime between 1922 and 1925, *J. californica* S. Watson (California black walnut), a species restricted to coastal southern California (Santa Barbara Co. to Orange Co.), and *J. hindsii* Rehd.[14] (Hinds black walnut), which ranges farther north along the east slopes of the Napa range to Walnut and Lafayette creeks, Contra Costa Co., were reported to be hosts of *completa* (Boyce, 1929, 1934).

The occurrence of *completa* in peaches (*Prunus persica* (L.) Batsch) in Utah (Anonymous, 1962) and California (Anonymous, 1964) is not surprising. The peach, as already mentioned, appears to be highly susceptible to fruit fly attack under certain conditions.

Distribution (Map 7). The distribution of *R. completa* reaches its most northeastern limit in southern Minnesota. It ranges southward along the transition zone, in sympatry with *R. suavis*, to Texas and possibly northern Mexico, and westward to central New Mexico. I have also seen one unlabeled specimen of *completa* from Mississippi, indicating that the species may extend its range farther eastward in the southern limits of its range than it does in the north.

Rhagoletis juglandis Cresson

Rhagoletis juglandis Cresson, 1920, Ent. News, 31: 65–66. [Holotype examined: ♂, Carr Canyon, Huachuca Mts., Ariz., July–Aug., 1919 (C. R. Biederman) (ANSP, No. 6235); paratypes examined: 11 ♂ ♂, same data as holotype.] —Cresson, 1929, Trans. Amer. Ent. Soc., 55: 413, pl. 16, fig. 11 (redescription, in key). —Boyce, 1934, Hilgardia, 8: 376–377, figs. 4C, 13, 14 (redescription, notes on biology). —Phillips, 1946, Mem. Amer. Ent. Soc., 12: 27, 67–68, figs. 25, 70, 128, 172 (larval morphology, in key).

Diagnosis. *R. juglandis* is easily recognized by its entirely light yellow coloring, complete absence of body markings, and

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[14] *J. hindsii* has recently been considered a variant of *J. californica* by Manning (1957), but the status of these two species is still in doubt (Manning, *in litt.*).

characteristic wing pattern (Fig. 195) which distinguishes it from other known species of *Rhagoletis*. The basal crossband is lacking or present only as a faint brownish yellow shading in the region of the humeral crossvein and over cell m.

Description. Body and wing measurements in Tables 10A–10B. Smallest representative of *suavis* group; no sexual dimorphism in body markings except for abdominal pollinose cream colored band along posterior margin of tergites II–IV in male and II–V in female. *Head* (Fig. 31): frontalia and parafrontalia light yellowish orange, ocellar plate brownish black, gulamentum and postgenae light cream, latter grading to dark yellowish orange dorsally; mentum golden tan; all other regions yellowish cream. Occipital, postorbital (6–13), postvertical (0–1), intravertical (0–1), genal, and well developed gular bristles dark yellowish orange; all other bristles black. *Thorax*: dorsum golden tan evenly covered with decumbent light yellow setae and whitish yellow microtrichia not arranged in vertical bands. Dorsocentrals slightly behind anterior supraalars; two pairs cream to light yellow scapulars. All pleural and sternopleural regions yellowish orange except for slightly lighter cream colored notopleural stripe. Two mesopleural bristles of about equal size. Halteres lemon yellow. Scutellum whitish with slight tint of yellow near base; postscutellum yellowish orange. A black spot above base of wing. *Legs*: all segments yellowish cream. Setae and bristles dark yellowish orange except variable black to yellowish cream postventral row of bristles on femur I; spurs on tibia II black; a single row of straight, short, dark yellowish orange setae on anterior-outer surface of tibia III, the latter also with short spur on anterior apex. *Wing* (Fig. 195): pattern distinctive in having no basal crossband. Apical band usually not joined to subapical band on costal margin; fuscated areas present along veins R_{4+5} and M_{1+2} between subapical and apical bands, these areas normally not joined to either crossband. Junction of R_{2+3} and R_{4+5} with up to two setae on dorsal surface, one seta on ventral surface; R_{4+5} with up to five setae on dorsal surface. Crossvein r-m slightly closer to m than M_3. Anal cell strongly pointed. *Abdomen*: all segments light cream without black markings. Some specimens with gray to brown appearance caused by internal decomposition. A faint lighter cream colored band present along posterior margin of tergites II–IV in male and II–IV or V in female. *Genitalia*: *male*— epandrium and surstyli (Figs. 72, 99) cream to light yellow; aedeagus (Fig. 130) resembling *suavis* (Fig. 129) with a finger-like apical appendage covered with short setae at tip; genital ring pouch well developed; phallic apodeme straight, surstyli straight, not bent at prensisetae. Ejaculatory apodeme normal (Fig. 142). *Female*—variation in ovipositor length in Fig. 20; ovipositor sheath golden yellow; three slightly club-shaped spermathecae with minute appressed scale-like papillae (Fig. 160); ovipositor with two pairs preapical setae.

Geographical variation. All specimens studied were from either Arizona or New Mexico, with the exception of one male from northern Utah and a female from southern Durango, Mexico. No geographical variation in body size was noted other than the normal wide variation common in this group.

Chromosome number and morphology (Fig. 221). The diploid number is 12; the MCA number is 22 as there are five pairs of metakinetic chromosomes and a single pair of acrokinetic dot chromosomes. No morphologically differentiated heterochromosomes (XY) or secondary constrictions were observed.

Source of cytological material: *J. major*, Indian Creek Campground, 6 mi. S. of Prescott, Arizona, 6,000 ft., 27 Aug. 1961; Southwest Research Station, Chiricahua Mts., Cochise Co., Arizona, 30 Aug. 1961; Nombre de Dios, Durango, Mexico, 6500 feet., 6 Sept. 1961.

Parasites. An *Opius* species near *ferru-gineus* Gahan (Hymenoptera, Braconidae) and a *Eucolia* species (Hymenoptera, Cynipidae) have been collected in Arizona from walnuts heavily infested with *jug-landis* (Flanders, 1961, personal communication). Both of these genera have species which parasitize *Rhagoletis;* therefore, it is likely that the two species mentioned are associated with *juglandis.*

Hosts. This species has been reared from *Juglans regia* L. variety in Arizona (Cresson, 1920; Brooks, 1921; Boyce, 1934; and others). *J. major* (Torr.) Heller (= *rupestris* of authors) has also been recorded as a host by Boyce (1934), and I have been able to rear *juglandis* from the fruits of this host collected in Arizona and Nombre de Dios, Durango, Mexico.

R. juglandis is sympatric with *boycei* over part of its range in Arizona and both of these species utilize the same species of *Juglans.*[15] A discussion of the relationships between the two species and their hosts will be found in the host section of *boycei.*

Distribution (Map 7). *R. juglandis* normally reaches its northernmost limits in Arizona and southwestern New Mexico. Its range extends southward along the Sierra Madre Occidental as far south as at least southern Durango and possibly farther whenever suitable hosts are available. The single record from Utah probably represents a recent extension of the northern limits of *juglandis* as walnuts are not native to this area and have only recently been introduced for commercial and ornamental purposes.

Rhagoletis boycei Cresson

Rhagoletis boycei Cresson, 1929, Trans. Amer. Ent. Soc., 55: 413, pl. 16, fig. 10. [Holotype examined: ♂, Carr Canyon, Huachuca Mts., Cochise Co., Arizona, 13 August 1929, Persian walnut (A. M. Boyce) (ANSP, No. 6342); paratypes examined: 1 ♂ 1 ♀, same data as holotype.] —Boyce, 1934, Hilgardia, 8: 377–378, figs. 4D, 13, 15 (redescription, notes on biology).

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[15] See Manning (1957) for recent revision of *Juglans* in Mexico and southwestern United States.

Diagnosis. *R. boycei* is the only black species in the walnut infesting group. It can also be easily distinguished from all other *Rhagoletis* by the typical wing pattern (Fig. 194) which bears some resemblance to its closest relative, *zoqui* (Fig. 196), and to *juglandis* (Fig. 195). The presence of black vertical bands on the postgenae and lateral margins of the postcranium are also features found in no other members of the *suavis* group. The anal cell is not as pointed in this species, nor is the genital ring pouch as conspicuous as in other members of the species group.

Description. Body and wing measurements in Tables 10A–10B. *Head* (Fig. 27): upper medial part of postcranium light yellow grading to tan ventrally; postgenae and lateral margins of postcranium black, anterior margins of postgenae yellowish cream grading to white dorsally. Postorbital regions cream; lower half of frontalia dark yellowish orange grading to lighter yellow dorsally; parafrontalia cream; face, parafacialia, and genae dark yellowish orange; gulamentum light yellow; ocellar plate and mentum black. Postvertical, occipital, genal, and weakly differentiated gular bristles light yellow; all other major bristles, including 7–13 postorbitals, black. *Thorax:* all regions black except for cream colored notopleural stripe, halteres, and scutellum, the latter tinged with black near base; postscutellum shining black. Dorsum covered with cream colored to light yellow setae and microtrichia, without vertical banded pattern; dorsocentrals slightly behind anterior supraalars; two pairs deep cream to cream colored scapular bristles; two mesopleural bristles of about equal size. *Legs:* coxae black, trochanters light yellow, femora and bristles black, except knees which grade to golden yellow. Semierect setae on anterior surface of femur II absent, though present in other members of this species group. Tibiae I and II light yellow with black shading; tibia III black grading to yellow at apices; about 6 to 10 strongly developed semierect black setae on

anterior surface. All tarsal segments light yellow. *Wing* (Fig. 194): similar to *juglandis* and *zoqui* in having fuscated areas on veins R_{4+5} and M_{1+2} between apical and subapical bands. Medial band not reaching posterior margin of wing as in *zoqui*. Usually one seta ventrally and two setae dorsally at junction of veins R_{2+3} and R_{4+5}, occasionally both absent; R_{4+5} with 4–5 setae on dorsal surface. Anal cell bluntly pointed, not as well developed as in other members of this species group. Crossvein r-m closer to m than M_3. *Abdomen*: all segments black in both male and female with tergites II–IV in male (Fig. 65) and II–V in female (Fig. 66) with white band on posterior margin; tergite V of male sometimes with yellowish orange area at apex. Both sexes sometimes with two narrow white spots on either side of medial line along posterior margin of tergite I. *Genitalia*: *male*—epandrium black, surstyli golden brown (Figs. 76, 95); aedeagus (Fig. 132) with rake-like appendage at tip resembling *completa* and *zoqui;* genital ring pouch small, not as strongly developed as in other members of *suavis* complex; phallic apodeme straight. Ejaculatory apodeme normal (Fig. 144). *Female*—variation in ovipositor length shown in Figure 20; ovipositor sheath shining black. Three cylindrical spermathecae with minute appressed scale-like papillae (Fig. 161) similar to those of *suavis* and *completa;* ovipositor with two pairs of minute preapical setae.

Geographical variation. The specimens examined were all from Arizona and other than a wide range in the size of individuals from the same locality no trends were found between individuals from different areas within the state.

Chromosome number and morphology (Fig. 222). The diploid number is 12; the MCA number is 22 as there are five pairs of metakinetic and a single pair of acrokinetic dot chromosomes. No morphologically distinguishable heterochromosomes or secondary constrictions were noted.

Source of cytological material: *Juglans major,* Onion Saddle Pass, Cochise Co., Arizona, 7500 ft., 30 Aug. 1961.

Courtship behavior. The courtship behavior of this species was not studied. Males were found patrolling ripe walnuts as do *suavis* and *completa* and are probably territorial.

Hosts. R. *boycei* has been reared from *Juglans major* (Torr.) Heller (= *rupestris* of authors, see Manning, 1957) and *J. regia* L. variety (Cresson, 1929; Boyce, 1934).

Distribution (Map 7). R. *boycei* apparently has a spotty distribution in Arizona and is more difficult to locate than the sympatric walnut infesting species, *juglandis.* I was able to locate a heavy infestation of *boycei* only at Onion Saddle Pass, Arizona, where *juglandis* appears to be abundant below 5,000–6,000 ft., and *boycei* above this altitude. The extent of overlap and emergence peaks were not determined. R. *boycei* has been collected in Arizona at altitudes up to 9,000 ft., and probably infests the native Arizona black walnut at its maximum altitude. Boyce (1934) was able to collect *juglandis* and *boycei* from the same grove, but I was unable to locate sympatric populations. This species apparently is restricted to southwestern New Mexico and Arizona and northern Sonora, Mexico.

Rhagoletis zoqui[16] new species

Types. Holotype ♂, Zacualtipan, Hidalgo, Mexico, 15 Sept. 1961 (G. L. Bush) (MCZ, No. 30827); paratypes: 10 ♂ ♂ 10 ♀ ♀, Zoquizoquipan, Hidalgo, Mexico, 29 Oct. 1960 (USDA Mex. Fruit Fly Lab.) (MCZ).

Diagnosis. Differs from *boycei,* its nearest relative, in being much larger (Tables 10A–10B) and in having the black areas of the body reduced to only the pleural and sternopleural areas of the thorax in the male. The rest of the body ranges from

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[16] This name represents a noun in apposition with the abbreviation of Zoquizoquipan, the place where the species was first collected.

tan to yellow. In the female, the black markings are limited to isolated spotting on the pleural regions. The dorsum in both sexes is golden tan. The wing pattern is similar to that of *boycei* (Figs. 194, 196) but is more extensively marked along veins R_{4+5} and M_{1+2} between the apical and subapical bands and bears a third horizontal marking in cell R_5 between the fuscous markings along R_{4+5} and M_{1+2}. All three horizontal bands may or may not be joined to the apical and subapical crossbands.

Description. Body and wing measurements in Tables 10A–10B. *Head* (Fig. 29): postcranium and frons yellowish orange; face slightly deeper yellow; mentum and postgenae tan, latter grading to yellowish orange dorsally. Postvertical, postorbital (5–12), and genal bristles black; occipital and well developed gular bristles yellowish orange; all other bristles black. *Thorax*: *male*—dorsum golden tan, covered by yellowish orange to yellowish tan setae and microtrichia not forming pattern of vertical stripes; dorsocentrals slightly behind anterior supraalars; two pairs yellowish orange scapular bristles with outer pair occasionally black, medial pair sometimes doubled. Two mesopleural bristles of about equal length. Pleural and sternopleural regions predominantly black. Notopleural stripe and scutellum light yellow, the latter grading to yellowish orange at base; postscutellum with two broad reddish brown vertical bands; halteres yellowish orange. *Female*—dorsum, scutellum, postscutellum, notopleural stripe, and halteres as in male. Pleural region not as heavily marked with black, predominantly yellowish tan; black markings usually limited to small isolated patches. The intensity of markings in some heavily marked females approaching coloration of some lightly pigmented males. *Legs: male*—coxae I and II dark shining brown; coxa III yellowish orange with brown markings on posterior surface. Trochanters yellowish orange. All bristles black. Femora black grading to yellowish orange at extremities; femur II with row of

semierect short bristles on anterior surface. Tibiae I and II tan grading to dark tan or black at base. Tibia III black with extremities grading to yellowish orange, with row of approximately 15 well developed semierect bristles along anterior outer margins. *Female*—all segments yellow to yellowish orange with black bristles, in striking contrast to those of male. *Wing* (Fig. 196): similar to pattern of *boycei* but with fuscous markings along R_{4+5} and M_{1+2} sometimes joined to crossbands. A third transverse band present in cell R_5 parallel to fuscous marking on R_{4+5} and M_{1+2}. Junction of apical and subapical crossbands on costa in cell R_1 constricted, much narrower than normal width of either crossband, occasionally completely separated by hyaline area as in *juglandis*. Up to three setae dorsally and usually two setae ventrally at junction of R_{2+3} and R_{4+5}; four to eight setae on dorsal surface of R_{4+5}. Anal cell strongly pointed, with r-m closer to crossvein m than to M_3. *Abdomen: male* (Fig. 61)—tergites II–IV with white band along posterior margin; tergites I–II yellowish orange, tergite III yellowish orange with two broad brownish black ovoid spots on either side of medial line; tergite IV mostly black, usually with some yellowish orange on medial line and outer margins; tergite V entirely brownish black. *Female* (Fig. 62)—tergites yellowish orange without brownish black markings; tergites II–V with white band along posterior margin. *Genitalia: male*—epandrium brownish black, surstyli dark yellowish orange (Figs. 78, 98); genital ring pouch well developed; phallic apodeme straight; aedeagus with rake-like apical appendage (Fig. 133); vesica bifurcate. Ejaculatory apodeme normal (Fig. 143). *Female*—variation in ovipositor length shown in Figure 20; ovipositor sheath dark brown. Three cylindrical spermathecae, tips somewhat pointed (Fig. 159), one usually about half as long as other two. Two pairs minute preapical setae on ovipositor tip.

Chromosome number and morphology

(Fig. 223). The diploid number is 12; the MCA number is 22 as there are five pairs of metakinetic chromosomes and a single pair of acrokinetic dot chromosomes. No morphologically differentiated heterochromosomes (XY) or secondary constrictions were observed.

Source of cytological material: *Juglans mollis*, Zoquizoquipan, Hidalgo, Mexico, Oct. 1957, and Sept. 15, 1961.

Courtship behavior. Males were found patrolling on walnuts, indicating that this species is territorial. No courtship behavior was observed.

Parasites. No parasites were reared from the material collected on two separate occasions at Zoquizoquipan, Mexico.

Hosts. This species has been reared only from *Juglans mollis* Engelm. (Nogal, Nogal encarcelada, nuez meca). Manning (1957) lists the known distribution for this species of walnut as Nuevo Leon, Tamaulipas, San Luis Potosi, Guanajuato, and Puebla, Mexico. It is apparently not sympatric with any other species of *Juglans* in Mexico. An infestation of larvae resembling *zoqui* was also found near Cuernavaca, Mexico, July 31, 1962, on what is probably *J. major* var. *glabrata* (Manning, 1963, *in litt.*).

Distribution (Map 7). Known only from the type locality and the nearby settlement Zoquizoquipan, Hidalgo, Mexico.

TABELLARIA SPECIES GROUP

Benjamin (1934) was the first to suggest that Cresson's 1929 revision of the genus *Rhagoletis* lumped too extensively. This is particularly true in the case of the *tabellaria* group where Cresson recognized only one species, *tabellaria*, and regarded *juniperina* and *ribicola* as mere "varieties" that did not merit recognition under a separate name. Careful examination reveals that Cresson's "varieties" are actually quite distinct and include representatives from two species groups. These groups seem to be either convergent for several characters such as wing pattern and body coloration,

or have retained these features through parallel evolution.

The *tabellaria* group consists of four species: *tabellaria, juniperina, persimilis,* and *ebbettsi.* This is probably a conservative number; *tabellaria* itself may prove to represent two sibling species when more is known about its biology (see host section of *tabellaria*). *R. ribicola*, regarded by Cresson as a synonym of *tabellaria*, is now placed in a group of its own in which *berberis* tentatively has been included. There is good morphological evidence that both groups probably originated in the Old World and may include several Eurasian species, but the affinities are as yet unclear.

Diagnosis. The *tabellaria* group is distinguished from the *ribicola* group on the basis of genitalic characters. In the *tabellaria* group the spermathecae are globular and attached to the spermathecal ducts by a well sclerotized cylindrical tube (Figs. 162–165). This is in contrast to the long cylindrical spermathecae of the *ribicola* group (Figs. 166–167). There are always three spermathecal ducts, but the number of spermathecae may vary from two to three. The aedeagus is also distinctive (Figs. 123–125). The vesica is somewhat convoluted in the *tabellaria* group and there is, at most, only a very small finger-like apical appendage which is never setulose. In *ribicola* and *berberis* the aedeagus has a relatively large finger-like apical appendage which is covered by well developed straight setae; the vesica is smooth (Figs. 126–127).

The *tabellaria* group can be distinguished from all other *Rhagoletis* groups by its wing pattern, genitalia, and body coloration.

Rhagoletis tabellaria (Fitch)

Tephritus tabellaria Fitch, 1855, Trans. New York State Agr. Soc., 1854, 14: 770. [Type lost.][17] —Fitch, 1856, 1st and 3rd Rept., Noxious and Beneficial Insects of New York: 66 (reprint of 1855 paper).

[17] A neotype was not designated pending a more complete study of both the eastern and western populations of this species.

			R. prasperata	R. persimilis
			:	.
HL	.74±.?? (.51-.89)	.64±.011 (.56-.86)	.78 (.68-.90)	.96 (.92-1.00)
HW	1.24±.040 (.77-1.38)	1.11±.031 (.88-1.23)	1.33 (1.03-1.57)	1.42 (1.38-1.50)
HH	1.09±.034 (.66-1.17)	.91±.027 (.73-1.05)	1.10 (.87-1.28)	1.23 (1.16-1.28)
EW	.57±.019 (.35-.66)	.51±.014 (.42-.58)	.72 (.53-.80)	.63 (.62-.65)
EH	.82±.028 (.52-.99)	.73±.021 (.62-.83)	.88 (.70-1.04)	.99 (.97-1.03)
FrWA	.48±.017 (.30-.57)	.43±.013 (.34-.53)	.44 (.34-.66)	.57 (.56-.60)
AL	.42±.013 (.28-.47)	.39±.011 (.33-.45)	.41 (.36-.45)	.47 (.45-.50)
IL	.58±.019 (.40-.65)	.49±.016 (.40-.60)	.61 (.51-.71)	.66 (.62-.69)
GW	.17±.009 (.10-.20)	.16±.007 (.11-.21)	.20 (.15-.25)	.19 (.17-.21)
FL	1.57±.056 (.95-1.82)	1.35±.046 (1.06-1.64)	1.79 (1.23-1.85)	1.98 (1.88-2.09)
	11	14	10	5
ML	?.??±.0?? (2.91-3.40)	2.86±.077 (2.37-3.37)	2.45±.070 (2.11-2.79)	?.46 (3.42-3.52)
MW	1.70±.036 (1.50-1.90)	1.53±.048 (1.21-1.80)	1.27±.028 (1.16-1.44)	1.72 (1.64-1.80)

Table 11A.   Body and wing measurements of males of
the tabellaria species group.   Figures represent
mean, standard error, and range.

	R. tabellaria East. pop.	R. tabellaria West. pop.	R. prasperata	R. persimilis
	6	12	16	7
HL	.77 (.65-.87)	.73±.016 (.64-.79)	.82±.025 (.61-.96)	1.01 (.93-1.07)
HW	1.27 (1.16-1.38)	1.19±.021 (1.05-1.28)	1.37±.043 (1.10-1.68)	1.53 (1.47-1.55)
HH	1.02 (.83-1.12)	.97±.029 (.73-1.05)	1.11±.036 (.91-1.35)	1.29 (1.24-1.36)
EW	.59 (.51-.62)	.55±.012 (.46-.63)	.68±.021 (.53-.83)	.68 (.65-.70)
EH	.83 (.70-1.93)	.79±.020 (.67-.87)	.91±.027 (.73-1.10)	1.05 (1.03-1.08)
FrWA	.48 (.37-.56)	.45±.013 (.38-.51)	.54±.024 (.40-.71)	.60 (.56-.64)
AL	.42 (.36-.50)	.40±.008 (.35-.43)	.43±.009 (.37-.49)	.50 (.48-.51)
IL	.56 (.45-.62)	.53±.013 (.46-.60)	.66±.022 (.50-.80)	.79 (.75-.83)
GW	.16 (.12-.20)	.15±.006 (.12-.19)	.21±.009 (.16-.25)	.21 (.19-.25)
FL	1.66 (1.44-1.81)	1.48±.037 (1.28-1.69)	1.70±.061 (1.33-2.08)	2.11 (2.03-2.20)
	6	12	11	.
ML	3.36 (3.07-3.70)	3.19±.068 (2.70-3.70)	2.84±.065 (2.59-3.42)	3.80 (3.46-3.96)
MW	1.84 (1.64-2.06)	1.75±.052 (1.41-2.13)	?.50±.048 (1.24-1.79)	2.03 (1.76-2.14)

Table 11B.   Body and wing measurements of females
of the tabellaria species group.   Figures represent
mean, standard error, and range.

(*Trypeta*) *tabellaria*, —Loew, 1862, Smithson. Misc. Coll., 6: 60.

Trypeta (*Rhagoletis*) *tabellaria*, —Loew, 1873, Smithson. Misc. Coll., 11: 263–265, 329, 338–339 (redescription).

Rhagoletis tabellaria, —Doane, 1898, Ent. News, 9: 69 (in key). —Aldrich, 1909, Canad. Ent., 41: 69 (in key). —Bezzi, 1911, Boll. Lab. Zool. Portici, 5: 18 (in key, distribution). —Phillips, 1923, J. New York Ent. Soc., 31: 122, 134 (in key, wing figured). —Cresson, 1929, Trans. Amer. Ent. Soc., 55: 406–407 (redescription, in key, wing figured). —Curran, 1932, Amer. Mus. Nov., 526: 3, 5 (in key, wing figured). —Pickett, 1937, Canad. J. Res. (D), 15: 62 (genitalia).

Diagnosis. R. *tabellaria* is distinguished from all other North American *Rhagoletis* species by the following characters: (1) the apical end of the phallotheca bears a tubular sac (Fig. 123, S); (2) there are three spermathecal ducts but only two globular spermathecae (Fig. 162); (3) the basal and medial wing bands are diffusely coalesced over a broad area along the posterior margin of the wing (Fig. 197); (4) the femora are predominantly black; (5) there is a horseshoe-shaped black marking on the posterior surface of the head. The only species with which *tabellaria* can be confused is *persimilis*, which has three conical, pine-cone shaped spermathecae (Fig. 165) and lacks the tubular sac on the apex of the phallotheca.

Description. Body and wing measurements in Tables 11A–11B. *Head* (Fig. 34): postcranial and posterior two-thirds of postgenal regions forming a brownish black horseshoe shaped pattern; mentum and ocellar plate brownish black; antennae and lower half of frons yellowish orange, parafacials slightly lighter (light yellow to white); face and parafacialia white, densely covered with microtrichia; genae, anterior margin of postgenae, and postorbital regions white, occasionally faintly tinted with yellow. Occipital and hair-like gular bristles light yellow, all other bristles black, including weak genal bristle; 5–12 postorbitals; postverticals short, often lacking; single intravertical usually present. *Thorax* (Fig. 46): dorsum brownish black to black

with four well defined parallel vertical stripes; outer pair broken by transverse sulcus, posterior section reaching line drawn between posterior supraalars; medial pair reaching from scapulars to base of prescutellars. Dorsocentrals in line with anterior supraalars; two pairs black scapular bristles, each pair occasionally with extra smaller bristles arranged in tandem; usually one mesopleural bristle; a second, much smaller, lower bristle occasionally present, variable in size. Notopleural stripe and circular scutellar spot white, latter extending from apex to a line drawn between basal scutellars; postscutellum shining black; halteres light tan to yellow. *Legs*: coxae and femora mostly black, femur I with some yellowish orange on anterior apical surface. Trochanters, tarsi, and all tibiae almost entirely light yellow; tibiae II and III with black shading near base; single row of stout semierect black setae on outer anterior surface of tibia III. *Wing* (Fig. 197): pattern consisting of two V's, one of which is inverted; basal and medial bands coalesce over broad area between anal cell and posterior margin of wing; apical and subapical bands joined on costa; hyaline region between apical band and costa. Junction of R_{2+3} and R_{4+5} bare; R_{4+5} bare over entire length. Anal cell sharply pointed (Fig. 180). *Abdomen* (Figs. 57–58): all segments brownish black to black with posterior margin of tergites II–IV in male, II–V in female with white to grayish white band. *Genitalia*: *male*—epandrium black, surstyli dark yellowish orange, of uniform width over most of length, tapering abruptly to blunt point near apex (Figs. 85, 101); end of phallotheca at junction with aedeagus with gland-like tubular sac (Fig. 123, S); vesica convoluted; aedeagal tip bearing small, narrow, finger-like appendage, most easily observed with phase contrast optics; ejaculatory apodeme normal (Fig. 146). *Female*—variation in ovipositor length shown in Figure 17; ovipositor with two pairs minute preapical setae; ovipositor sheath black; three sper-

mathecal ducts and two globular sperma-
thecae with thickened bases; spermathecae
covered with long scale-like papillae (Fig.
162).

Geographical variation. No differences
in either size (see Tables 11A–11B) or
color pattern were noted between the
eastern and western populations of this
species.

Chromosome number and morphology
(Fig. 226). The diploid number in both
sexes is 12; the MCA number is 22 as there
are five pairs of metakinetic chromosomes
and a single pair of acrokinetic dot chromo-
somes. No secondary constrictions or mor-
phologically differentiated heterochromo-
somes (XY) were observed.

Source of cytological material: *Cornus
amomum*, Blue Hills, vicinity Milton, Mass.,
4 July 1963; *Vaccinium* spp., vicinity Monte-
sano, Wash., 16 July 1961.

Hosts. The eastern population of *tabel-
laria* has been found associated only with
the genus *Cornus* (Cornaceae). Glasgow
(1933) reported infestations in *C. stolonif-
era* Michx., and I have been able to
rear it from *C. amomum* Mill. growing in
the vicinity of Boston, Mass. *C. amomum*
is also infested by *R. cornivora* (Hall,
1943), a member of the *pomonella* group,
but I have not found the two *Rhagoletis*
species infesting berries on the same plant.
However, there is a single specimen of
tabellaria in a series from the CNC which
Hall reared from *C. amomum* during his
studies on *cornivora* in Canada (Hall, 1938,
1943). This would indicate that mixed pop-
ulations of these two species may possibly
occur.

The western representatives of *tabellaria*
apparently infest only the fruits of *Vaccin-
ium* (Ericaceae) (Plank, 1923; Phillips,
1946) (for details of distribution see Camp,
1942). *Cornus* is not known to be attacked
by *tabellaria* west of the 98th meridian,
although the same species serving as hosts
in the East occur all the way to the west
coast. Ecological factors other than host
specificity must restrict eastern *tabellaria*

to the more mesophytic regions of north-
eastern North America.

The eastern population is also appar-
ently unable to infest *Vaccinium*, or is ex-
cluded from this host by the presence of
mendax (*pomonella* group). *R. mendax*,
however, does not occur over the entire
range of eastern *tabellaria*, and *tabellaria*
seems to have no trouble holding its own
against the other sympatric competing
Cornus infesting species, *cornivora* (*pomo-
nella* group). Competitive exclusion, there-
fore, does not seem to be the explanation
for the difference in host preference be-
tween the two allopatric *tabellaria* popula-
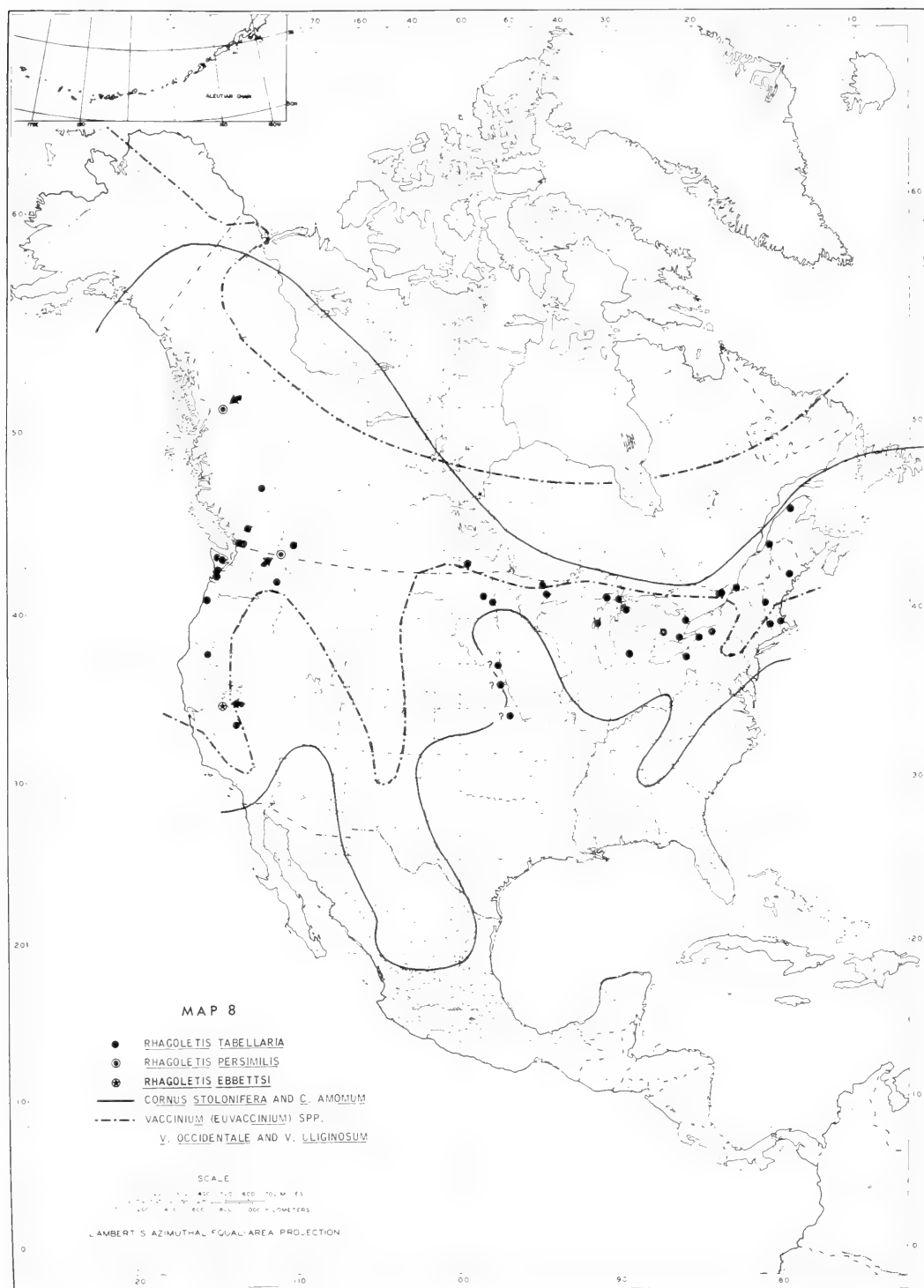tions.

These two allopatric populations prob-
ably represent distinct species even though
morphological differences were not de-
tected. Sibling species pairs showing sim-
ilar amphicontinental distributional pat-
terns are found in other *Rhagoletis* groups,
such as *pomonella–zephyria* and *cingulata–
indifferens*, which infest either closely re-
lated or different hosts.

Further details regarding the distribution
and history of *Cornus* and *Vaccinium* may
be found in the host sections of *cornivora*
and *mendax*.

Distribution (Map 8). *R. tabellaria* is
represented by two distinct allopatric and
allotrophic populations. The northernmost
limits of the eastern race appear to coincide
with the northern limits of its host,
Cornus. As with many eastern spe-
cies of *Rhagoletis*, its western limits
do not extend beyond the 100th me-
ridian. Its southern limits are less well
known, and it may occur farther south
than indicated on the map. The three lo-
calities accompanied by question marks
represent single individuals which are
somewhat morphologically distinct from
both the eastern and western populations
and may represent a third distinct species.
In the absence of suitable material or ac-
companying host data, I have included
them with *tabellaria*.

The distribution of the western race is

MAP 8

• RHAGOLETIS TABELLARIA
⊙ RHAGOLETIS PERSIMILIS
⊛ RHAGOLETIS EBBETTSI
—— CORNUS STOLONIFERA AND C. AMOMUM
—·—·— VACCINIUM (EUVACCINIUM) SPP.
V. OCCIDENTALE AND V. ULIGINOSUM

SCALE

LAMBERT'S AZIMUTHAL EQUAL-AREA PROJECTION

more spotty and probably extends farther north and east.

Rhagoletis juniperina Marcovitch

Rhagoletis juniperinus Marcovitch, 1915, Ann. Ent. Soc. Amer., 8: 171–173, pl. 13, figs. 4–7. [Lectotype ♂, by present designation, Six Mile Creek, Ithaca, N.Y. (MCZ, No. 7723; cotype, CU, No. 510.2).] —Phillips, 1923, J. New York Ent. Soc., 31: 134, 135, pl. 18, fig. 19 (in key, host). —Phillips, 1946, Mem. Amer. Ent. Soc., 12: 26, 69–70, figs. 26, 71, 129, 130, 173 (larval morphology, in key). —Hering, 1958, Stuttgarter Beitr. z. Naturkunde, 7: 4 (comparison with R. flavigenualis).
Rhagoletis tabellaria, —Cresson, 1929 (in part), Trans. Amer. Ent. Soc., 55: 406–407 (variety of tabellaria).
Rhagoletis juniperina, —Rohdendorf, 1961, Ent. Obozr., 40: 176 (justified emendation of incorrect original spelling).

Diagnosis. The following combination of characters distinguish *juniperina* from other members of the *tabellaria* and *ribicola* groups: (1) basal and medial wing bands are not joined along the posterior margin of the wing; (2) there is no black shading on the posterior lower lateral half of the head; (3) all femora are black; (4) the surstyli are straight, short and sharply pointed (Fig. 83); (5) the spermathecae are globular and covered by many small sharply pointed scale-like papillae (Fig. 163).

Description. Body and wing measurements in Tables 11A–11B. *Head* (Fig. 36): black stripe across lower two-thirds of postcranium but not extending ventrally over postgenae. Postorbitals, upper one-third of postcranium, and lower half of frons light yellowish orange; parafrontalia, face including parafacialia, genae, and gulamentum bright yellow; postgenae light yellow grading to slightly darker dorsally; mentum black. Occipital and genal bristles light yellow, all other major head bristles black; postverticals short, about as long as postorbitals (8–12); gular bristle not differentiated from other yellow setae on gulamentum and postgenal regions. *Thorax* (Fig. 44): all regions concolorous black except for white notopleural stripe and scutellar spot. Dorsum covered evenly with white to light yellow setae and microtrichia arranged in four faintly differentiated vertical rows, medial pair sometimes fused into single broad band; dorsocentrals slightly before a line drawn between anterior supraalars; two pairs yellowish orange scapular bristles; two mesopleural bristles. Circular scutellar spot small, extending from apex between bases of apical scutellars cephalad to a point about one-half to two-thirds distance between apical and basal scutellar bristles. Postscutellum shining black; halteres light yellowish orange. *Legs*: variable in color, depending on locality. Coxae and femora black, latter ranging to yellow at knees to almost entirely yellow in some specimens from Manitoba. Trochanters brownish yellow; tibiae yellowish tan; tibia II with weak row of setae on outer posterior surface; tibia III bearing short row of semierect setae on outer anterior surface. *Wing* (Fig. 198): medial band not joined to either basal or subapical bands; hyaline area between apical band and costa. R_{4+5} bare; 0–3 setae at junction of R_{2+3} and R_{4+5} (0 in most eastern specimens, 1–3 in specimens from California). Crossvein r-m equidistant from m and M_3. Anal cell pointed (Fig. 178). *Abdomen*: as in *tabellaria* (see Figs. 57, 58); base color dark brown to brownish black, posterior margin of tergites II–IV in male, and II–V in female with whitish pollinose band. *Genitalia*: *male*—epandrium black, surstyli yellowish orange, straight and sharply pointed, slightly narrowed between prensisetae and base (Figs. 83, 103). Aedeagus without apical appendage (Fig. 125); vesica smooth; ejaculatory apodeme normal (Fig. 150). *Female*—variation in ovipositor length shown in Figure 17; ovipositor sheath black, ovipositor tip with three minute preapical setae. Three spermathecal ducts; two globular spermathecae, each with large, somewhat barrel-shaped cylindrical base and covered by long sharply pointed scale-like papillae (Fig. 163).

Geographical variation. The specimens examined from California and Manitoba are markedly larger than those from eastern and southwestern United States (for example, see variation in ovipositor length, Fig. 17). The Manitoba specimens have more extensive areas of yellow markings on the legs, while those from California have a much larger scutellar spot and are the only specimens with one to three setae at the junction of R_{2+3} and R_{4+5}. They also have two or three mesopleural bristles instead of the usual one.

Chromosome number and morphology (Fig. 227). The diploid number is 12; the MCA number is 22 as there are five pairs of metakinetic chromosomes and a single pair of acrokinetic dot chromosomes. A secondary constriction was noted in early metaphase plates on the short arms of one chromosome pair. No heteromorphic sex chromosomes (XY) were observed.

Source of cytological material: *Juniperus virginiana*, Lincoln, Mass., Oct. 10, 1962.

Courtship behavior. The courtship behavior of this species has not been studied.

Hosts. R. *juniperina* and other species of Tephritidae which infest *Juniperus* (Cupressaceae) apparently restrict their attacks to species of Section *Sabina.* No tephritid, as far as is known, infests any species of Section *Oxycedrus.* R. *juniperina* has been reared from *Juniperus virginiana* L. at Ithaca, New York (Marcovitch, 1915; Phillips, 1946), and I have collected an adult and larvae from the same host in Lincoln, Mass. A single specimen of *juniperina* has also been reared from *J. monosperma* (Engelm.) Sarg. growing in Oak Creek Canyon, Arizona.

The presence of *juniperina* in Manitoba and California, beyond the range of its two recorded hosts, suggests that this fly infests other species of *Juniperus*, although no *Rhagoletis* have ever been recorded from juniper in the far western part of the United States. The host relationships of these western populations are therefore in doubt. The Manitoba and particularly the California populations may represent new species. *Rhagoletis flavigenualis*, whose wing pattern bears some resemblance to that of *juniperina*, has been reared from *J. excelsa* Bieb. (=*J. sabina* L. var. *taurica* Pall.) in Turkey (Hering, 1958). The only other species of Tephritidae associated with juniper is *Paraterellia varipennis* (Coquillett), which has been reared from *Juniperus occidentalia* Hook in California (Foote, 1960).

Section *Sabina* is widespread over North America (Map 9), Eurasia, and North Africa (see Florin, 1963, for details). Some North American species in the Section are closely related to Old World forms. This is true of *J. virginiana, J. horizontalis* Moench., and *J. scopulorum* Sarg., which Stebbins (1950) considers to be only well marked subspecies of the Old World *J. sabina.*

The past history of *Juniperus*, its present distribution in North America, and the existence of conspecific or closely related species in Eurasia and North America indicate that the genus was probably part of the Holarctic Arcto-Tertiary geoflora. Insects associated with juniper would undoubtedly follow a similar distributional pattern. On morphological grounds the closest relatives of *juniperina* appear to be Eurasian. It may therefore have arrived in North America sometime before or during the Pleistocene. It is also possible that *juniperina* arose from some North American *tabellaria*-like species. However, the morphology of *juniperina* is sufficiently different to suggest that it has not diverged recently from any North American representatives of the *tabellaria* group. The answer to this problem will have to await a study of the east Asiatic *Juniperus* and its associated insect species.

Distribution (Map 9). **CANADA:** MANITOBA: Carberry; vicinity of Stockton; Aweme. **U.S.A.:** MASSACHUSETTS: Lexington, Middlesex Co. NEW YORK: Ithaca, Tompkins Co. TEXAS: Schulenburg, Fayette Co. ARIZONA: Oak Creek Canyon,

MAP 9

●   RHAGOLETIS JUNIPERINA
───   JUNIPERUS SPP., SECTION SABINA
·········   JUNIPERUS VIRGINIANA

LAMBERT'S AZIMUTHAL EQUAL AREA PROJECTION
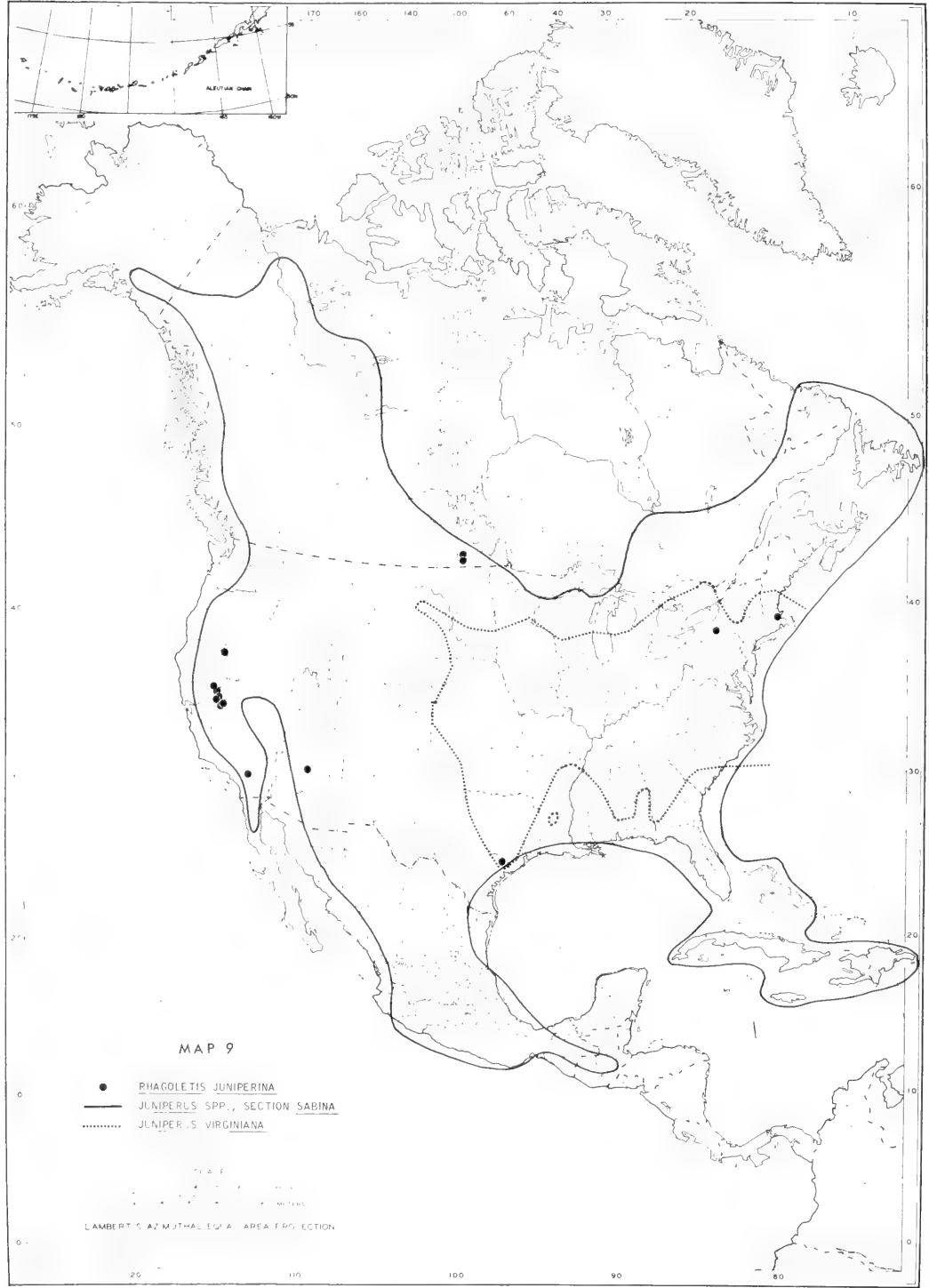
Coconino Co. CALIFORNIA: Lake City, Modoc Co.; Woodfords, Alpine Co.; Big Bear Lake, San Bernardino Co.; Glen Aulin to Waterwheel Falls, Yosemite National Park; Norden, Nevada Co.; vicinity of Leavitt Meadows and vicinity of Sonora Pass, Mono Co.; Silver Lake, Amador Co.; Cathedral Lake Tahoe.

Rhagoletis persimilis new species

Types. Holotype ♂, Robson, British Columbia, 15 June 1947 (H. R. Foxlee) (CNC, No. 8456); paratypes: 5 ♂ ♂ 6 ♀ ♀, same data as type (CNC, MCZ).

Diagnosis. Similar to *tabellaria* in color pattern but larger (Tables 11A–11B) and differing in the following characters: (1) longer ovipositor (Fig. 17); (2) there are three globular to somewhat cone-shaped spermathecae covered by small appressed scale-like papillae (Fig. 165); (3) the proctiger of the male is more elongate and densely covered with long fine setae near the apex (Fig. 86) resembling the proctiger of *Carpomyia vesuviana* A. Costa (see Silvestri, 1916); (4) the surstyli are more pointed and thicker at the base (Fig. 86) than those of *tabellaria* (Fig. 85); (5) the aedeagus (Fig. 124) is swollen medially, bears a small tuft of setae on the dorsal margin of the vesica, and has no gland at the apex of the phallotheca.

Description. Body and wing measurements in Tables 11A–11B. *Head* (Fig. 33): entire posterior surface black grading to dark brown to brownish yellow in region of gulamentum; postorbital region, genae, parafrontalia, and entire face white to whitish yellow; frons light yellow, antennae yellowish orange. Postocellars yellow, all other major bristles black; setae on postgenae and gulamentum white. Usually one postvertical, 8–13 postorbitals, usually three, occasionally four, pairs of lower frontal orbital bristles. *Thorax*: black except for white notopleural stripe and scutellar spot, latter with V-shaped anterior margin reaching anteriorly beyond line drawn between basal scutellars; lateral margins passing well

outside base of apical scutellars and ending below apex; postscutellum shining black, almost completely devoid of microtrichia; halteres yellow. One to two mesopleural bristles; anterior dorsocentrals located about in line with anterior supraalars; dorsum of thorax as in *tabellaria* (Fig. 46) with four distinct rows of white microtrichia and covered with yellow decumbent setae; outer row broken by transverse sulcus. *Legs*: all coxae and femora black; all tibiae yellow; trochanters I and II yellow, III yellow with black on posterior surface; tibia III with row of weakly developed semierect setae on anterior outer margin; tarsal segments yellow. *Wing* (Fig. 199): basal and medial bands joined broadly from middle to cell Cu_1. Preapical band joined to apical band from costa to just beyond R_{4+5}; hyaline area between apical band and costa. R_{4+5} and junction with R_{2+3} bare. Crossvein r-m about equidistant from m and M_3. Anal cell moderately pointed (Fig. 179). *Abdomen*: base color black with tergite V polished. Tergites I–IV in both sexes with white pollinose band along posterior margin; very narrow white band along posterior margin of tergite V in some females. *Genitalia: male*—epandrium black, surstyli yellow; proctiger elongate, densely covered with setae at apex; surstyli broad at base, tapering to sharp point (Fig. 86); fultella with distinct shelf behind base of curved phallic apodeme; aedeagus (Fig. 124) swollen medially; vesica with narrow finger-like appendage and small tuft of setae on dorsal margin; ejaculatory apodeme normal (Fig. 148). *Female*—variation in ovipositor length (Fig. 17); ovipositor with two pairs of preapical setae; ovipositor sheath shining black; three globular spermathecae somewhat cone-shaped, covered with very small scale-like papillae fused to surface; base enlarged and cylindrical.

Host. The host of this species is not known.

Distribution (Map 8). **CANADA:** BRITISH COLUMBIA: Bear Lake and Robson.

Rhagoletis ebbettsi new species

Type. Holotype ♀, 4 mi. E. Ebbetts Pass, Alpine Co., California, summer 1961 (R. P. Allen) (USNM, No. 67378); wing slide No. 313, ♀ genitalia No. 327 (G. L. Bush).

R. ebbettsi is being described from a single damaged specimen. The legs are missing, and the antennae and mouthparts are recessed into the head making it difficult to study details of these structures. The specimen is discolored from material used in NH_3 sticky traps.

Certain aspects of the wing pattern, spermathecae, and black markings on the posterior region of the head relate this species closely to *tabellaria* and *juniperina*.

Diagnosis. The striking wing pattern of *ebbettsi* (Fig. 200) in combination with the distinct pattern of the dorsum (Fig. 43) and globular spermathecae (Fig. 164) separate this species from all other North American *Rhagoletis*. The medial wing band is joined by a broad fuscous region in cell R_5 between R_{4+5} and M_{1+2} just apicad of r-m. The only species with which *ebbettsi* could be confused is *R. zernyi*, known only from the type specimen collected at Albarracin, Aragon, Spain in 1924 (Hendel, 1927). It can be differentiated from this species by the position of the connection between the subapical and medial crossbands. The posterior hyaline region between the medial and subapical bands reaches to R_{4+5}, completely bisecting cell R_5 in *zernyi*. In *ebbettsi* the junction covers cell R_5.

Description. Head: base color yellow, darkened and greasy, probably the result of residue from sticky trap. Postorbital and upper occipital regions yellow, rest of posterior surface of head with horseshoe shaped black mark grading to slightly brownish black ventrally; mentum black. Postverticals and gular bristles yellow, all other major bristles black, including small genal bristle; postgenae and gulamentum covered with scattered yellow setae; three postverticals on each side of occiput; outer-verticals, right innervertical, and lower left lower fronto-orbital missing. Six postorbitals on left and eight on right, some missing. *Thorax:* base color black, dorsum (Fig. 43) covered by light yellow decumbent setae and white pollinose microtrichia arranged in four rows, fused anteriorly; two inner rows shorter than outer pair. Notopleural stripe and scutellar spot cream, possibly tinted with yellow in normal specimens; scutellar spot reaching from below apex anteriorly to line drawn between basal scutellars; lateral margins passing through base of apical scutellars. Postscutellum shining black. Left haltere missing, right haltere tan. Two mesopleural bristles, upper missing. Dorsocentrals in line with anterior supraalars; left dorsocentral missing. *Legs:* all segments except black coxa and yellow right trochanter II missing. *Wing* (Fig. 200): basal band not joined to medial band; medial band joined to subapical band in cell R_5 between R_{2+3} and R_{4+5} apicad of r-m; hyaline area between apical band and costa. R_{4+5} bare over entire length and at junction with R_{2+3}. Anal cell bluntly pointed. Crossvein r-m about midway between m and M_3. *Abdomen:* black; tergites II–V with broad white pollinose bands along posterior margins as in *tabellaria* (Fig. 58). *Genitalia:* ovipositor with two preapical setae; 0.87 mm long, 0.18 mm wide; ovipositor sheath black. Two spermathecae covered by small appressed scale-like papillae, each with bulbous base and small apical knob (Fig. 164). Three spermathecal ducts.

Distribution (Map 8). Known only from the type locality.

RIBICOLA SPECIES GROUP

The *ribicola* group includes two species, *ribicola* and *berberis*. *R. berberis*, tentatively placed in this group, may actually be more closely related to certain European species which are also known to infest the genus *Mahonia* (*Berberis* of authors). *R. ribicola* was considered to be so closely related to *tabellaria* that Cresson (1929)

synonymized *ribicola* with *tabellaria*. The similarities, however, are only superficial. The two species in the *ribicola* group, particularly *ribicola* itself, seem to be more closely related to the *cingulata* group in North America and to *flavicincta* Loew in Europe.

Diagnosis. The characters which distinguish the *ribicola* group from the *tabellaria* group are restricted to the genitalia. Both *ribicola* and *berberis* have long cylindrical spermathecae covered with scattered, rather long scale-like papillae (Figs. 166–167). In members of the *tabellaria* group these organs are globular in shape (e.g., Fig. 162). The aedeagus in both *ribicola* and *berberis* has an apical appendage covered with short spike-like setae (Figs. 126–127). Members of the *tabellaria* group have no setulose apical appendage.

Rhagoletis ribicola Doane

Rhagoletis ribicola Doane, 1898, Ent. News, 9: 69–72. [Lectotype ♀, by present designation, (Washington Expt. Station No. 66) (USNM cotype No. 42213; MCZ type No. 17085).] — Aldrich, 1909, Canad. Ent., 41: 69, 72, pl. 4 (1) (in key). —Bezzi, 1911, Boll. Lab. Zool. Portici, 5: 7, 14-16, 19 (in key, discussion). —Marcovitch, 1915, Ann. Ent. Soc. Amer., 8: 173 (compared with *juniperina*). —Curran, 1932, Amer. Mus. Nov., 526: 3, 6–8. —Pickett, 1937, Canad. J. Res. (D), 15: 62 (genitalia). —Phillips, 1946, Mem. Amer. Ent. Soc., 12: 72–74, figs. 29, 74, 135, 176 (larval morphology, in key).
Rhagoletis tabellaria, —Cresson, 1929 (in part), Trans. Amer. Ent. Soc., 55: 406–407, pl. 16, fig. 5.

Diagnosis. There is a conspicuous sexual dimorphism in leg coloration of *ribicola* which Doane (1898) did not recognize in his original description. All segments except the coxae are yellow in the male, while in the female the coxae, as well as femora II and III are brownish black with yellowish knees. Femur I is entirely yellow or with brownish black shading on the posterior surface. This character, in combination with the wing pattern (Fig. 201), distinctive surstyli (Fig. 84), and strongly keeled ejaculatory apodeme (Fig. 147),

differentiates *ribicola* from *berberis* and all other North American *Rhagoletis*.

Description. Body and wing measurements in Tables 12A–12B. *Head* (Fig. 37): posterior region and mentum brownish black, with postorbital, upper occipital, and postgenal regions cream to white. Frons, face, and genae light yellow, antennae slightly yellowish orange. Postocellar and genal bristles yellow; all other major bristles, including 1–2 postverticals and 8–14 postorbitals, brownish black to black. Gular bristle not differentiated from light yellow setae on postgenae and gulamentum. *Thorax:* dark brownish black except for cream colored notopleural stripe and scutellar spot, latter reaching anteriorly beyond a line drawn between basal scutellars; lateral margins reaching well outside base of apical scutellars. Dorsum with distinct pattern of four white pollinose stripes similar to that of *berberis* and *tabellaria* (Fig. 46). Outer stripes reaching from scapulars to line between posterior pair of posterior supraalars, broken by transverse sulcus; inner pair shorter, ending just behind line between dorsocentrals; dorsocentrals slightly before line drawn between anterior supraalars; one mesopleural bristle. Postscutellum shining black; halteres yellow. *Legs: male*—coxae and spurs black, all other segments and bristles yellow, including row of semierect bristles on anterior surface of tibia III. *Female*—coxa I, trochanters, tibiae and tarsal segments yellow; coxae and femora II and III dark brown to brownish black, latter grading to yellow at apices; femur I usually entirely yellow, occasionally with brown shading on posterior surface. *Wing* (Fig. 201): medial band not reaching posterior margin and not joined to basal or subapical bands. Hyaline region between apical band and costa. R_{4+5} bare over entire length and at junction with R_{2+3}. Anal cell variable, not strongly pointed; crossvein Cu_2 sometimes only slightly bowed (Fig. 176). *Abdomen:* shining black with pollinose white band along posterior margin of tergites II–IV in

	R. ribdoa	R. beraetus	R. b..d.	R. stradella	R. fausta
n	16	?	10	10	10
HL	.68±.016 (.59-.73)	.74±.032 (.65-.78)	1.18±.023 (.97-1.26)	1.24±.047 (1.17-1.32)	.86±.025 (.81-.94)
HW	1.14±.024 (.95-1.21)	1.23±.001 (1.11-1.34)	1.70±.036 (1.41-1.83)	1.72±.022 (1.60-1.85)	1.28±.026 (1.11-1.37)
HH	.93±.033 (.75-1.06)	1.04±.024 (.90-1.19)	1.46±.039 (1.20-1.69)	1.61±.022 (1.53-1.74)	1.08±.023 (.95-1.15)
EW	.57±.010 (.51-.61)	.61±.009 (.52-.67)	.82±.018 (.68-.88)	.81±.010 (.76-.87)	.63±.013 (.55-.67)
EH	.76±.019 (.66-.82)	.83±.015 (.62-.92)	1.16±.030 (.94-1.27)	1.25±.017 (1.15-1.33)	.88±.020 (.77-.95)
FrWV	.44±.017 (.33-.50)	.46±.009 (.35-.51)	.65±.010 (.58-.69)	.73±.009 (.68-.78)	.46±.010 (.41-.51)
ML	.36±.006 (.31-.33)	.36±.001 (.32-.39)	.54±.008 (.48-.57)	.59±.010 (.53-.63)	.43±.011 (.37-.47)
FL	.52±.013 (.43-.56)	.57±.007 (.49-.64)	.79±.026 (.60-.90)	.99±.020 (.90-1.14)	.54±.029 (.50-.62)
GW	.17±.008 (.13-.22)	.18±.001 (.13-.20)	.25±.001 (.22-.27)	.35±.008 (.31-.38)	.18±.008 (.15-.23)
TL	1.30±.048 (1.01-1.52)	1.44±.028 (1.26-1.60)	2.44±.067 (2.05-2.70)	2.29±.032 (2.17-2.46)	1.70±.042 (1.44-1.82)
	10	1.	10	10	10
W..	2.74±.040 (2.05-2.44)	2.66±.02. (2.32-2.78)	4.41±.096 (3.75-4.73)	.±.052 (3.71-4.20)	.28±.090 (3.00-3.65)
WW	1.14±.025 (.99-1.24)	1.40±.013 (1.28-1.50)	1.97±.050 (1.60-2.14)	1.94±.025 (1.82-2.06)	1.51±.036 (1.34-1.70)

Table 12A. Body and leg measurements of males of the *ribdoa* species group and miscellaneous species. Figures represent mean, standard error, and range.

	R. ribdoa	R. beraetus	R. b..d.	R. stradella	R. fausta
n	10	13	10	10	10
HL	.76±.016 (.61-.79)	.82±.016 (.70-.89)	1.22±.026 (1.07-1.34)	1.33±.028 (1.16-1.43)	.94±.015 (.85-1.00)
HW	1.21±.024 (1.02-1.32)	1.36±.029 (1.19-1.43)	.7±.06. (1.55-1.91)	1.87±.033 (1.64-1.96)	1.43±.029 (1.22-1.51)
HH	.99±.023 (.84-1.12)	1.15±.028 (.97-1.28)	1.47±.038 (1.23-1.62)	1.73±.040 (1.50-1.86)	1.17±.021 (1.02-1.27)
EW	.62±.013 (.53-.69)	.68±.014 (.57-.75)	.87±.032 (.76-.93)	.85±.017 (.72-.91)	.70±.016 (.60-.76)
EH	.82±.018 (.65-.90)	.9±.01. (.78-1.01)	1.24±.031 (1.03-1.35)	1.35±.023 (1.19-1.46)	.97±.020 (.82-1.04)
FrWV	.48±.013 (.39-.54)	.52±.012 (.44-.56)	.±.01. (.-.)	.80±.018 (.69-.87)	.49±.025 (.45-.54)
ML	.39±.00. (.33-.41)	.41±.001 (.36-.46)	.56±.012 (.50-.62)	.62±.011 (.56-.68)	.47±.008 (.42-.52)
FL	.55±.008 (.49-.58)	.66±.013 (.57-.70)	.±.01. (.-.)	1.07±.032 (.86-1.20)	.59±.027 (.55-.64)
GW	.18±.005 (.15-.22)	.21±.014 (.16-.27)	.22±.001 (.17-.27)	.38±.015 (.31-.46)	.18±.006 (.15-.21)
TL	1.45±.050 (1.08-1.54)	1.63±.044 (1.35-1.83)	2.62±.064 (.-.)	2.69±.065 (2.27-2.87)	1.99±.046 (1.65-2.13)
	10	12	11	11	11
	3.00±.079 (2.75-3.33)	2.86±.069 (2.39-3.09)	.±.06. (4.1-5.14)	4.79±.068 (4.43-5.08)	3.60±.100 (3.09-4.15)
WW	1.47±.038 (1.27-1.62)	1.58±.041 (1.31-1.73)	2.27±.051 (1.90-2.59)	2.34±.043 (2.07-2.51)	1.74±.056 (1.50-2.06)

Table 12B. Body and leg measurements of females of the *ribdoa* species group and miscellaneous species. Figures represent mean, standard error, and range.

male, and II–V in female as in *tabellaria* (Figs. 57–58). *Genitalia: male*—epandrium (Figs. 84, 104) black; surstyli yellow, straight; phallic apodeme sharply curved and flared apically; ejaculatory apodeme (Fig. 147) with heavily sclerotized keel along apical end; aedeagus (Fig. 127) with setulose apical appendage; vesica not well developed. *Female*—variation in ovipositor length shown in Figure 17; ovipositor with two minute preapical setae; ovipositor sheath shining black. Three spermathecal ducts and two twisted cylindrical spermathecae (Fig. 167) sparsely covered with scale-like papillae.

Chromosome number and morphology (Fig. 228). The diploid number in both sexes is 12; the MCA number is 22 as there are five pairs of metakinetic chromosomes and a single pair of acrokinetic dot chromosomes. No secondary constrictions or morphologically differentiated heterochromosomes (XY) were observed.

Source of cytological material: *Ribes* spp., Burns, Harvey Co., Oregon, 4199 ft., July 28, 1961.

Courtship behavior. This species was not studied under field conditions. In the laboratory, males readily courted females without the presence of host fruit. It is therefore not known if *ribicola* males are territorial. In plastic observation chambers, males would actively court females with a characteristic wing flicking consisting of a rapid forward movement followed by a rapid upward jerk. The male, upon sighting the female, rapidly turns in her direction. This movement is usually followed by several wing flicking movements to which the female responds with a similar, but not identical, rapid wing movement. The male then crouches and slowly stalks the female, weaving back and forth as he moves. Upon reaching the female, but without touching her, he flies onto her back and attempts copulation. If the female is ready to mate she spreads her wings, lifts her abdomen, and extrudes her ovipositor. No licking or tapping which has been reported for many *Drosophila* (Spieth, 1952) was ever seen in the courtship of *ribicola*. Males would actively court females through a plastic partition, but would not court males. This indicates that the male is capable of recognizing the female on strictly visual cues without the use of pheromones.

Hosts. R. *ribicola* has been reared from both wild and cultivated currants and gooseberries, including *Ribes aureum* Pursh (Phillips, 1946), R. *grossularia* L. and R. *vulgare* (Piper and Doane, 1898). This species seems to limit itself strictly to members of the genus *Ribes* (Saxifragaceae). A single specimen of *ribicola* from Guadalupe, California, bearing a label "ex strawberry," probably was not reared from this fruit. The same seems to be true of a specimen of *berberis* bearing the same locality, date, and host record. Both specimens appear to have spent some time in a McPhail trap, although there are no labels to this effect. They are covered with a white film typical of insects removed from a liquid trap using fermenting lure.

The host relationships of this species are so poorly known that no attempt was made to plot the distribution of the individual species of *Ribes*. Map 10 shows the general distribution of *Ribes* spp. in North America and gives some idea of the distribution of *ribicola* in relation to its potential host species.

Distribution (Map 10). **CANADA:** BRITISH COLUMBIA: Lillooet. **U.S.A.:** IDAHO: Moscow, Latah Co. WYOMING: Big Horn Co. WASHINGTON: Washington Expt. Stations No. 020, No. 66; Chehalis, Lewis Co.; Opportunity, Spokane Co. OREGON: Burns, Harvey Co. CALIFORNIA: Guadalupe, Santa Barbara Co.

Note on California distribution. All of the California specimens referred to *ribicola* by Foote and Blanc (1963) that I have examined are *juniperina* and are treated with that species. Specimens of *ribicola* recorded by Foote and Blanc from the following localities were not examined: Woodfords, Alpine Co.; Echo Lake, El Dorado

MAP 10

● RHAGOLETIS RIBICOLA
— RIBES SPP.

SCALE

LAMBERT'S AZIMUTHAL EQUAL AREA PROJECTION

Co.; Tioga Pass, Mono Co.; Dunsmuir, Siskiyou Co.; Mineralking, Tulare Co.; Dardanelles, Tuolumne Co. The only record of *ribicola* in California that I have been able to definitely establish on purely morphological grounds is the single male from Guadalupe. Chromosomes studied from larvae removed from the fruit of *Ribes* spp. near McCloud, Siskiyou Co., California on Aug. 2, 1961, proved to be different from those of *ribicola* in both morphology and number (2n=10 vs. 2n=12 for *ribicola*). The larvae were probably those of *Epochra canadensis* (Loew), a species which occurs over most of California (Foote and Blanc, 1963). Adults were not reared from this collection.

Rhagoletis berberis Curran

Rhagoletis berberis Curran, 1932, Amer. Mus. Nov., 526: 6, 8. [Holotype examined: ♀, Hood River, Oregon, June 23, 1931, *Berberis nervosa* Pursh. (AMNH); ♂ allotype, Hood River, Oregon, July 30, 1930 (AMNH); 3 ♂ ♂ paratypes, same data as allotype.] — Pickett, 1937, Canad. J. Res. (D), 15: 60 (genitalia). —Phillips, 1946, Mem. Amer. Ent. Soc., 12: 26, 61–62, figs. 20, 65, 120, 121, 167 (larval morphology, in key).

Diagnosis. The entirely black body, characteristic wing pattern (Fig. 202), genitalia (Figs. 87, 106, 126, 149), and karyotype (Figs. 229–230) make it easy to distinguish this species from all other North American representatives of *Rhagoletis*. The apical band of the wing is contiguous with the costa and not separated from it by a hyaline region as in *ribicola* and members of the *tabellaria* group. *R. berberis*, with a karyotype consisting of 12 autosomes and a heteromorphic sex chromosome pair, is the only member of the genus *Rhagoletis* thus far studied with a diploid number of 14.

Description. Body and wing measurements in Tables 12A–12B. *Head* (Fig. 35): posterior region dark brownish black to black except for yellow upper occiput and dark cream postorbital region. Frons and antennae yellow, parafrontalia and face cream to white; parafacialia and genae light yellow, latter grading to white posteriorly; occasional individuals may have these areas slightly tinted with red; mentum black. Genal and postocellar bristles yellowish brown to black; all other major bristles, including single intravertical and 5–9 postorbitals, black; gular bristles not differentiated from rest of light yellow bristles on postgenae and gulamentum. *Thorax*: black; mesonotum with four rows of yellow decumbent setae and white pollinose microtrichia similar to that of *tabellaria* (Fig. 46); inner row shorter than outer row, latter broken at transverse sulcus. Dorsocentrals slightly before a line drawn between anterior supraalars; two mesopleural bristles. Notopleural stripe and scutellar spot cream tinted with yellow, latter reaching anteriorly from below apex to a line drawn between basal scutellars; lateral margins passing outside base of apical scutellars. Postscutellum shining black; halteres cream grading to light yellow at base, or entirely light yellow. *Legs*: coxae, trochanters, and femora brownish black, latter yellow at apices. Tibiae I and II yellow, Tibia III brownish black, slightly bowed with row of stout semierect setae on anterior outer surface. All tarsal segments yellow. *Wing* (Fig. 202): medial band not reaching posterior margin and not joined to basal or subapical crossbands. Apical band contiguous with costa over entire length. R_{4+5} bare, with a seta dorsally at junction with R_{2+3}. Crossvein r-m about midway between m and M_3. Anal cell bluntly pointed (Fig. 177). *Abdomen*: all segments black with white pollinose band along posterior margin of tergites II–IV in both sexes, some females with narrow white band on posterior margin of tergite V as in *tabellaria* (Figs. 57–58). *Genitalia*: male—epandrium black; surstyli yellow, tapering to sharp point (Figs. 87, 106); dorsal margin of surstyli serrated near base; phallic apodeme straight, aedeagus with long apical appendage covered at tip with short setae (Fig. 126); vesica hood-like; ejaculatory apodeme normal

(Fig. 149). *Female*—variation in ovipositor length shown in Figure 17; ovipositor with two minute preapical setae; ovipositor sheath shining black. Two spermathecal ducts and two cylindrical spermathecae covered with only a few scattered scale-like papillae (Fig. 166).

Chromosome number and morphology (Figs. 229–230). The diploid number is 14; the MCA number is 23 in the male and 24 in the female. The male karyotype consists of four pairs of metakinetic autosomes and two pairs of acrokinetic autosomes, as well as a metakinetic X and an acrokinetic Y dot sex chromosome. In the female karyotype there are four pairs of metakinetic autosomes, two pairs of acrokinetic autosomes, and a single pair of metakinetic X chromosomes. The acrokinetics were verified through the study of late metaphase and early anaphase figures in which the kinetichores were just beginning their advance to the poles. A secondary constriction was always noted at metaphase in the short arm of the longest metakinetic autosome (Figs. 229–230).

Source of cytological material: *Mahonia nervosa*, Shaw, Oregon, 22 July 1961.

Courtship behavior. Males of *berberis* were frequently seen patrolling berries of Oregon grape, which suggests that this species, like many other *Rhagoletis*, is territorial, and courtship probably occurs on or near fruit of the host plant.

Hosts. R. berberis has been reared from *Mahonia nervosa* (Pursh) Nutt. (Berberidaceae) or Oregon grape (Curran, 1932), which occurs in the coniferous forest and humid transition zone from Vancouver Island, British Columbia, to Monterey, California. I have also examined specimens reared from *Mahonia aquifolium* (Pursh.) Nutt. A single specimen from California bearing the label "ex strawberry" is probably an error. It appears to have been taken in a liquid bait trap (for details see *ribicola, Hosts*). There are several other species of native northwestern *Mahonia* which may also serve as hosts for *berberis*.

The host relationships of *berberis* are too poorly known to reach any definite conclusions about its origin, though like *ribicola*, it seems to be more closely related to Eurasian *Rhagoletis* such as *berberides* Benedek and possibly *cerasi* (*sensu lato*), both of which infest *Mahonia*. The present distribution of *berberis* and its association with *M. nervosa* suggest that it is probably a recent arrival from eastern Asia. *M. nervosa* is the only representative of the *Orientales* group (Section *Longibracteatae*) in the Western Hemisphere, a group restricted to southeastern Asia (Ahrendt, 1961). A careful search for related species of *Rhagoletis* infesting *Berberis* and *Mahonia* in eastern Asia could help to establish the origin and affinities of *berberis*.

Distribution (Map 11). **CANADA:** BRITISH COLUMBIA: Langford; Robson; Summerland; Vancouver. **U.S.A.:** WASHINGTON: N. Bonneville, Skamania Co.; Wenatchee, Chelan Co.; Puyallup and La Grande (Univ. of Wash. Demonstration Forest), Pierce Co.; Kettle Falls, Stevens Co.; Walla Walla, Walla Walla Co.; Seattle, King Co.; Juniper Beach; Glen Elum. OREGON: Hood River, Hood River Co.; Corvallis, Benton Co.; Shaw, Macleay, Marion Co. CALIFORNIA: Susanville, Lassen Co.; Etna, Dunsmuir, Horse Creek, Happy Camp, Yreka, Siskiyou Co.; Guadalupe, Santa Barbara Co.

MISCELLANEOUS SPECIES

Rhagoletis basiola (Osten Sacken)

Trypeta flavonotata,[18] —Loew, 1873, Smithson. Misc. Coll., 256: 244 (Yukon River, Alaska). —Coquillett, 1899, J. New York Ent. Soc., 7: 261 (syn. *Zonosema basiolum* and *Spilographa setosa*).

Trypeta (Zonosema) basiolum Osten Sacken, 1877, U.S. Geol. and Geogr. Survey Bull., 3: 348. [Cotypes examined: ♀, lectotype by present designation, Brookline, Mass. (MCZ, No. 10244); ♀, Collins, Idaho, 27 July 1898 (J. M. Aldrich Coll.) (USNM, No. 43546; MCZ, No. 17081).]

Spilographa setosa Doane, 1899, J. New York

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[18] *Trypeta flavonotata* Macquart is synonymous with *Zonosemata electa* (Say) (see Stone, 1951).

MAP 11

● RHAGOLETIS BERBERIS
○ LOCALITIES CITED IN LITERATURE

SCALE

LAMBERT S AZIMUTHAL EQUAL-AREA PROJECTION
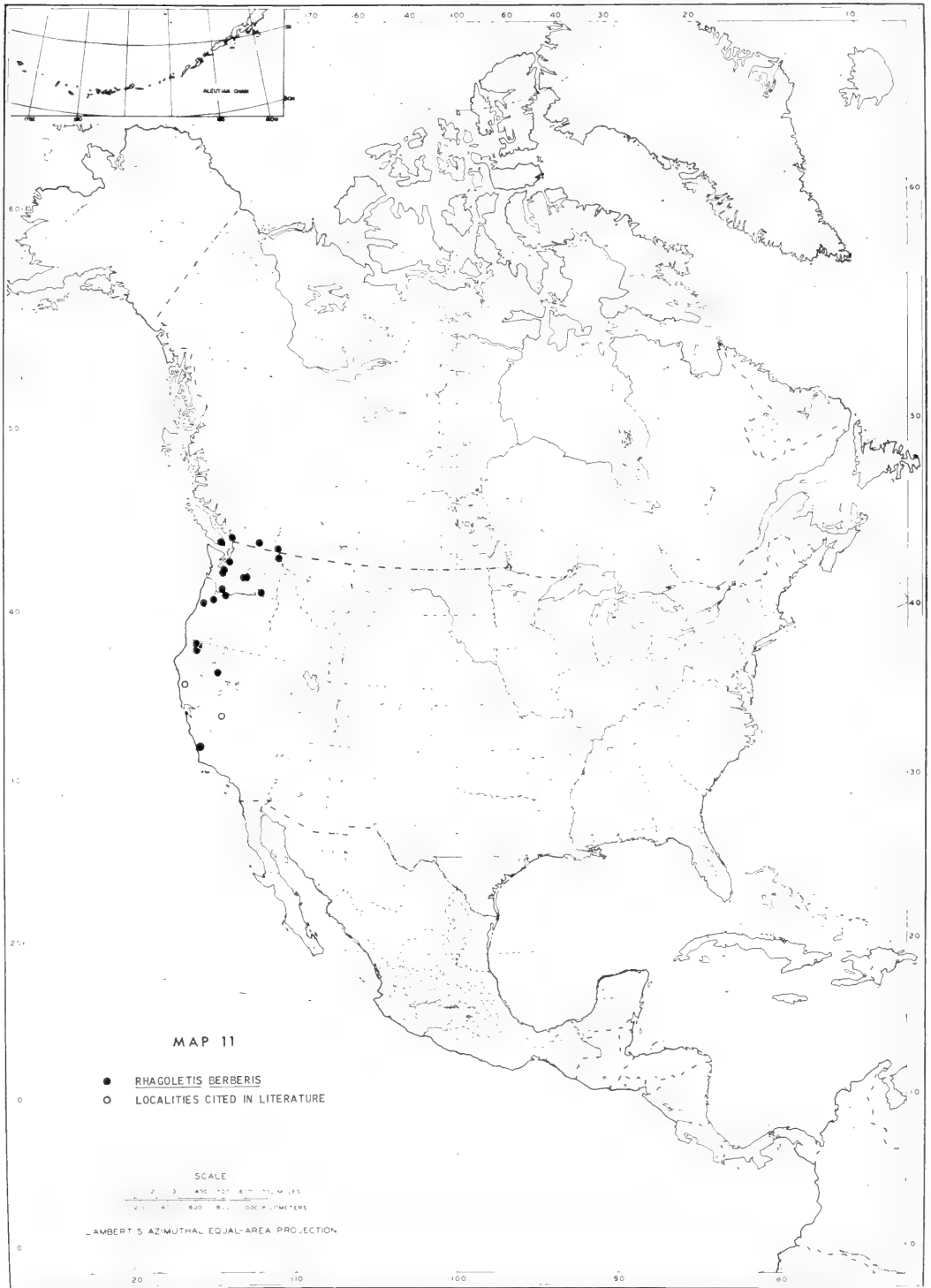
Ent. Soc., 7: 178–179, pl. 3, fig. 1. [Cotypes examined: ♀, Vollmer, Idaho, 31 July 1898 (USNM, No. 43546), designated lectotype by Stone, 1951; ♂, Pullman, Wash., 2 Aug. 1898 (AMNH, No. 16113).]

Spilographa basiolum, —Aldrich, 1905, Smithson. Misc. Coll., 46: 604.

Zonosema flavonotata, —Phillips, 1923, J. New York Ent. Soc., 31: 128, pl. 28, fig. 9 (in key, distribution; = *Zonosema basiolum* Osten Sacken).

Zonosema setosa, —Phillips, 1923, J. New York Ent. Soc., 31: 128, pl. 28, fig. 10 (in key, distribution). —Benjamin, 1934, U.S. Dept. Agr. Tech. Bull., 401: 18 (discussion of synonymy).

Zonosemata setosa, —Phillips, 1946, Mem. Amer. Ent. Soc., 12: 98–100, figs. 45, 87, 192 (larval morphology, in key).

Rhagoletis basiola, —Stone, 1951, Proc. Ent. Soc. Wash., 53: 45–48 (nomenclatorial history). —Balduf, 1959, Illinois Biol. Monogr., 26: 1–194 (biology, description).

R. basiola is the only representative in the Western Hemisphere of the *alternata* species group, which includes five described Eurasian species. Species in this group infest the fruits of *Rosa* (Rosaceae), *Berberis* (Berberidaceae), and *Lonicera* (Caprifoliaceae). Some authors have considered the *alternata* group to represent a distinct genus (Loew, 1862; Collin, 1947; Rohdendorf, 1961) (see Introduction for details).

R. basiola is most closely related to *alternata*, and until recently they were considered conspecific. Stone (1951), however, found consistent differences between the Palearctic and Nearctic populations, and concluded that they should be regarded as distinct species. He has also presented a résumé of the nomenclatorial history of this species.

Certain morphological characters of *basiola*, such as light body coloration, wing pattern, and position of dorsocentral bristles, suggest a possible relationship with both South American *R. ferruginea* Hendel and the Nearctic genus *Zonosemata* Benjamin.

Diagnosis. *R. basiola* is distinguished from *alternata* in having the apical wing band usually joined to the subapical crossband (Fig. 212). In *alternata*, these two

bands are usually separated (Fig. 208). The pattern of the postscutellum also offers a useful character for the separation of the two species. In *basiola*, there are two highly variable, small, circular or triangular-shaped dark brown spots (Figs. 173–174) with their broad bases on the dorsal margin of the postscutellum and ending on or near the lower margin. The bands on the postscutellum of *alternata* are broad, never triangular-shaped (Fig. 175), and are much wider than the medial yellow stripe.

Description. Body and wing measurements in Tables 12A–12B. Entirely yellow species, except for dark brown markings on postscutellum, fuscous wing bands, and distinct black spot on mesonotum just above base of wing. *Head* (Fig. 38): posterior surface light yellow; antennae and frons darker yellowish orange; face and genae yellowish white; mentum yellow. All major head bristles light brown to yellow; 1–2 postverticals, 7–14 postorbitals. *Thorax*: all regions including scutellum light yellow except for lighter cream-colored notopleural stripe; scutellum without scutellar spot; postscutellum with two variable black circular or triangular spots (Figs. 173–174) usually beginning broadly along dorsal margin of postscutellum and ending on or well before lower margin. Dorsum covered with yellow decumbent setae and yellow pollinose microtrichia not arranged in definite pattern; two pairs yellow scapular bristles, sometimes individually doubled with smaller second bristles located in tandem behind primary bristles; major bristles generally brownish black to brown; dorsocentrals well behind anterior supraalars, but slightly closer to anterior supraalars than anterior pair of posterior supraalars; two mesopleural bristles of about equal size. *Legs*: all segments light yellow. Tibia II with distinct row of five to six semierect stout setae along outer posterior margin; tibia III with row of well developed semierect setae on outer anterior surface. *Wing* (Fig. 212): pattern similar to that of *Zonosemata electa* and to several European

species in *alternata* group. Basal band narrow, medial band not reaching posterior margin of wing and not joined to either weakly developed basal or well developed subapical bands; stigma more heavily infuscated than rest of medial band; small triangular-shaped intercalary band beginning on costa about midway between apical and subapical bands, reaching posteriorly and ending on or near vein R_{4+5}; apical band usually joined to subapical band though somewhat narrowed at junction in most specimens; occasional individuals with these bands separated by hyaline area. R_{4+5} setulose with 1–3 setae at junction with R_{2+3}. Crossvein r-m slightly closer to M_3 than to m. Anal cell pointed. *Abdomen*: all segments yellowish tan, slightly darker than thorax. *Genitalia*: *male*— epandrium and surstyli yellowish tan, latter tapering beyond prensisetae to sharp point; phallic apodeme curved (Figs. 88, 96). Aedeagus (Fig. 128) with small finger-like apical appendage; vesica smooth. Ejaculatory apodeme normal (Fig. 139). *Female*—variation in ovipositor length shown in Figure 19; ovipositor short and broad, wider at middle than at base; ovipositor with two minute preapical setae; ovipositor sheath brownish orange. Three spermathecal ducts and two (rarely three) globular spermathecae covered with appressed, sharply pointed scale-like papillae (Fig. 169).

Geographical variation. No geographical variation was noted in the morphology of this species.

Chromosome number and morphology (Figs. 231–233). The diploid number in both sexes is 10; the MCA number is 18 as in anaphase there are five pairs of metakinetic or submetakinetic chromosomes, two pairs of which have very short, almost subtelokinetic arms (Fig. 231). In late prophase or early metaphase plates the large satellites that are so prominent in metaphase (Fig. 233, SAT) are often separated from the long arms of the chromosomes by a nucleolus, giving the appear-

ance of the karyotype typical of other *Rhagoletis* species. At first glance, the two satellites in this case appear as two dot chromosomes which, when counted as such, give a diploid number of 12. In anaphase (Fig. 232) the positions of the kineticore can be readily localized.

A distinct difference between the length of the arms of the longest chromosome pair was noted in anaphase configurations of some specimens. This heteromorphic chromosome pair probably represents the sex chromosome (Fig. 232).

Source of cytological material: *Rosa* spp., Lincoln, Mass., various dates in Sept. 1962.

Courtship behavior. I have not observed the courtship of this fly under laboratory or natural conditions. Balduf (1959) states that males are usually more conspicuous than females, mostly confining themselves to the undersides of leaves and the hips which indicates that this species may use the host fruit as a rendezvous for courtship. The flies apparently mate readily under laboratory conditions (Balduf, 1959), although I was unable to observe copulation in the few specimens I reared from Lincoln, Mass., and those sent to me from Minnesota by Dr. Balduf.

Parasites. Balduf found four species of hymenopterous parasites attacking the immature stages of *basiola*. One of these is known only from the larval stage, and Balduf tentatively identified it as a eupelmid (probably *Eupelmus* sp.). Two others, *Opius rosicola* Muesebeck and *O. baldufi* Muesebeck (Braconidae), occur sympatrically and are widely distributed over northern North America. *Halticoptera rosae* Burks (Pteromalidae), an egg parasite, has also been reared frequently from *basiola*.

Hosts. Balduf (1959) recently summarized the ecology of *R. basiola* and the closely related European species, *R. alternata*. It is through his efforts that so much is known about this species today.

A total of 19 species of *Rosa* have been recorded as hosts of *R. basiola*. These are listed in Table 13 with the localities in

TABLE 13. SPECIES OF *Rosa* FROM WHICH *R. basiola* HAS BEEN REARED. (FROM BALDUF, 1959)

Rosa spp.	Locality
R. acicularis Lindl.	N Canada, Alaska, NE Minn.
R. alcea Greene	B.C., Sask., Man.
R. arkansana Porter	Wisc.
R. blanda Ait.	NE Minn., Wisc., Ont.
R. canina L.	Ohio, Ind., Ill.
R. carolina L.	Wisc., Ohio, Ind., Ill.
R. eglanteria L.	N.C.
R. gallica L.	Ohio, Ind., Ill.
R. macounii Greene	NE Minn., B.C., Sask., Man., Neb.
R. nitida Willd	Maine
R. nutkana Presl.	B.C., Sask., Man., NW United States
R. palustris Marsh.	Ohio, Ind., Ill.
R. pyrifera Rydb.	B.C., Sask., Man.
R. rugosa Thund	R.I., N.Y.
R. setigera Michx.	Ohio, Ind., Ill.
R. spaldingii Crepin	NW United States
R. ultramontana (S. Wats.) Heller	NW United States
R. virginiana Mill.	Maine
R. woodsii Lindl.	B.C., Sask., Man., Utah

which they were collected. Balduf noted a considerable variation in the number of larvae per unit number of rose hips correlated with the latitude in which they were collected.

There was a steady decline in the ratio of larvae to hips from the northern to southern limits of the range, averaging 40–54 per cent in Ely, Minnesota, and only 4 per cent in central Illinois with some large samples completely devoid of infestation.

Distribution (Map 12). *R. basiola* has the widest range of any North American representative of *Rhagoletis*. Apparently it is better adapted to the cold temperate regions, occurring wherever favorable climatic conditions and suitable species of *Rosa* exist. The most northerly record is Miller House, 66 miles south of the Arctic Circle. Balduf (1959, p. 25) had no records of *basiola* south of latitude 35° N, but its presence in southern California at 35° 5′ (see Map 12) indicates that this species is capable of adjusting to rather moderate conditions of mild winters.

Rhagoletis striatella van der Wulp

Rhagoletis striatella van der Wulp, 1899, Biol. Cent. Amer., Dipt., 2: 408–409, tab. XI, fig. 30. [Type not examined, location unknown; ♀, Amula (now Amulango), Guerrero, Mexico.] —Bezzi, 1911, Boll. Lab. Zool. Portici, 5: 7, 14 (in key, description). —Phillips, 1923, J. New York Ent. Soc., 31: 135–136, pl. 18, fig. 27 (in key). —Cresson, 1929, Trans. Amer. Ent. Soc., 55: 405–406, pl. 16, fig. 3 (redescription, wing figured). —Curran, 1932, Amer. Mus. Nov., 526: 6 (in key). —Aczél, 1954, Dusenia, 5: 78 (in key).

Diagnosis. *R. striatella* is probably the most distinctive member of the genus in North America. Its extremely long ovipositor, broad genae, bulging postgenal regions, and wing pattern ally it closely to no other Holarctic species. It is more closely related to some of the South American species, such as *R. lycopersella, psalida,* and *ochraspis,* but differs from all described species of *Rhagoletis* in having a V-shaped scutellar spot, and two broad white pollinose stripes on the dorsum (Fig. 42). The wing pattern of *striatella* (Fig. 209), with the subapical band joined to the forked apical band forming the letter F, also serves to identify this species. Superficially, this pattern resembles that of *fausta* (Fig. 210), except that in *fausta* the subapical band is joined to the medial band. In *striatella,* these two bands are separated by a hyaline area.

Description. Body and wing measurements in Tables 12A–12B. *Head* (Fig. 41): posterior surface yellow; frons bright yellow; antennae more yellowish orange; face light yellow, covered with white pollinose microtrichia; genae yellow, postgenae and postorbital regions a lighter whitish yellow; mentum brownish black, haustellum heavily shaded with black. Genae with black setae along ventral margins and with a black shaded spot below eye; genal bristle yellow, all other major bristles black; gular bristle not differentiated from black to yellow setae on postgena and gulamentum; 1–5 intraverticals; 2–5 postverticals; 11–23 postorbitals. Three to four lower fronto-

MAP 12

●   RHAGOLETIS BASIOLA

○   LOCALITIES CITED IN LITERATURE

—— ROSA SPP.

SCALE

LAMBERT S AZIMUTHAL EQUAL-AREA PROJECTION
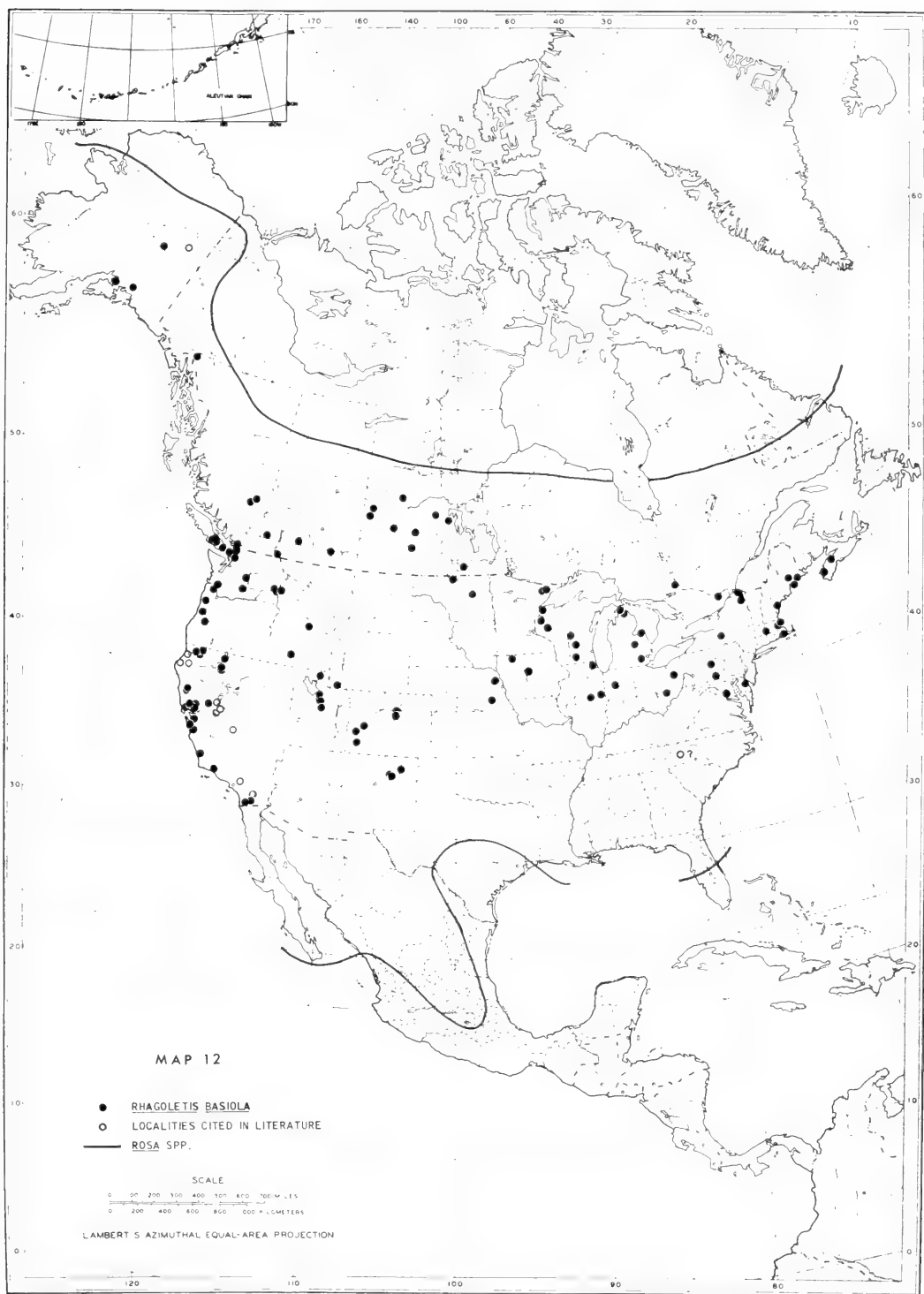
orbital bristles, variable. *Thorax* (Fig. 42): black except for cream colored notopleural stripe and V-shaped scutellar spot; post-scutellum black; halteres light lemon yellow, slightly darker at base. Dorsum covered with yellow to black decumbent setae and white pollinose microtrichia, latter arranged in two broad rows; usually two pairs of scapular bristles, sometimes individually doubled with second smaller bristles in tandem behind first; dorso-centrals slightly behind anterior supra-alars; two mesopleural bristles. *Legs*: coxae black; femora black except for yellow knees. All trochanters and tibiae I and II yellow, heavily shaded with black. Tibia III black. Tarsi dark yellow. *Wing* (Fig. 209): medial band not reaching hind margin nor joined to basal or subapical bands. Subapical band joined to forked apical band forming an F-shaped pattern. R_{4+5} with many setae on dorsal surface, occasionally with one or two on ventral surface. One to two setae dorsally at junction of R_{4+5} and R_{2+3}. Anal cell pointed. Crossvein r-m at midpoint between m and M_3. *Abdomen*: base color black with tergites polished. Tergites II–IV in male, and II–V in female with white pollinose band along posterior margin. *Genitalia*: *male*—epandrium black; sur-styli short and broad, yellow (Figs. 89, 105); hypopygium elongated; genital ring membrane with well developed pouch; ful-tella with a broad shelf behind base of phallic apodeme. Aedeagus (Fig. 134) long and narrow, with a long apical finger-like appendage; vesica smooth. Ejacula-tory apodeme normal, heavily pigmented (Fig. 140). *Female*—variation in oviposi-tor length shown in Figure 19; ovipositor long compared with other *Rhagoletis* species (Figs. 17–21, 182–183), with a dis-tinct subapical constriction (Fig. 184); ovipositor sheath shining black; two long preapical setae. Two spermathecal ducts; two globular spermathecae (Fig. 170) with small pointed appressed scale-like papillae. Base of spermatheca cylindrical; apex with nipple-like protuberance.

Egg. The egg of this species is not typical of other *Rhagoletis* species. The end bearing the micropyle is elongated rather than blunt as in all other species (Figs. 240–241).

Chromosome number and morphology (Figs. 234–235). The diploid number in the male is 11, and in the female 12. In this species there is a compound sex-determining mechanism consisting of a long acrokinetic X_1, a shorter acrokinetic X_2 bearing a distinct satellite, and a long acrokinetic, or possibly subacrokinetic, Y chromosome which is shorter than X_1 but longer than X_2. In addition to the hetero-morphic sex chromosomes, there are three pairs of metakinetic autosomes and a single pair of acrokinetic autosomes. Therefore, the MCA number in the male is 17, and in the female 18. Other than the satellite on the X_2, no other secondary constrictions were noted.

The remaining pair of short autosomes are acrokinetic. The dot chromosomes, nor-mally present in other *Rhagoletis* species, are not found in *striatella*. The satellites of the X_2 sex chromosomes, occasionally separated from the parent chromosomes during squashing, may be confused with dots in the karyotype of the female. Only one dot is present in the karyotype of the male.

Source of cytological material: *Physalis* sp., El Yukon, Mex., Mexico, 8,800 ft., Aug. 4, 1962.

Hosts. The first host record for *striatella* resulted from an interception by the U.S. Department of Agriculture at Brownsville, Texas, of infested husk tomatoes (*Physalis* sp., Solanaceae) from Mexico. *R. striatella* is reputed to cause considerable damage to cultivated husk tomatoes in Mexico, al-though its economic importance as a pest has not been documented. The distribu-tion of this species over much of central United States, southern Canada, and Mex-ico indicates that *striatella* probably infests several species of *Physalis* in different parts of its range.

MAP 13

● RHAGOLETIS STRIATELLA

○ TYPE LOCALITY

SCALE

LAMBERT'S AZIMUTHAL EQUAL-AREA PROJECTION
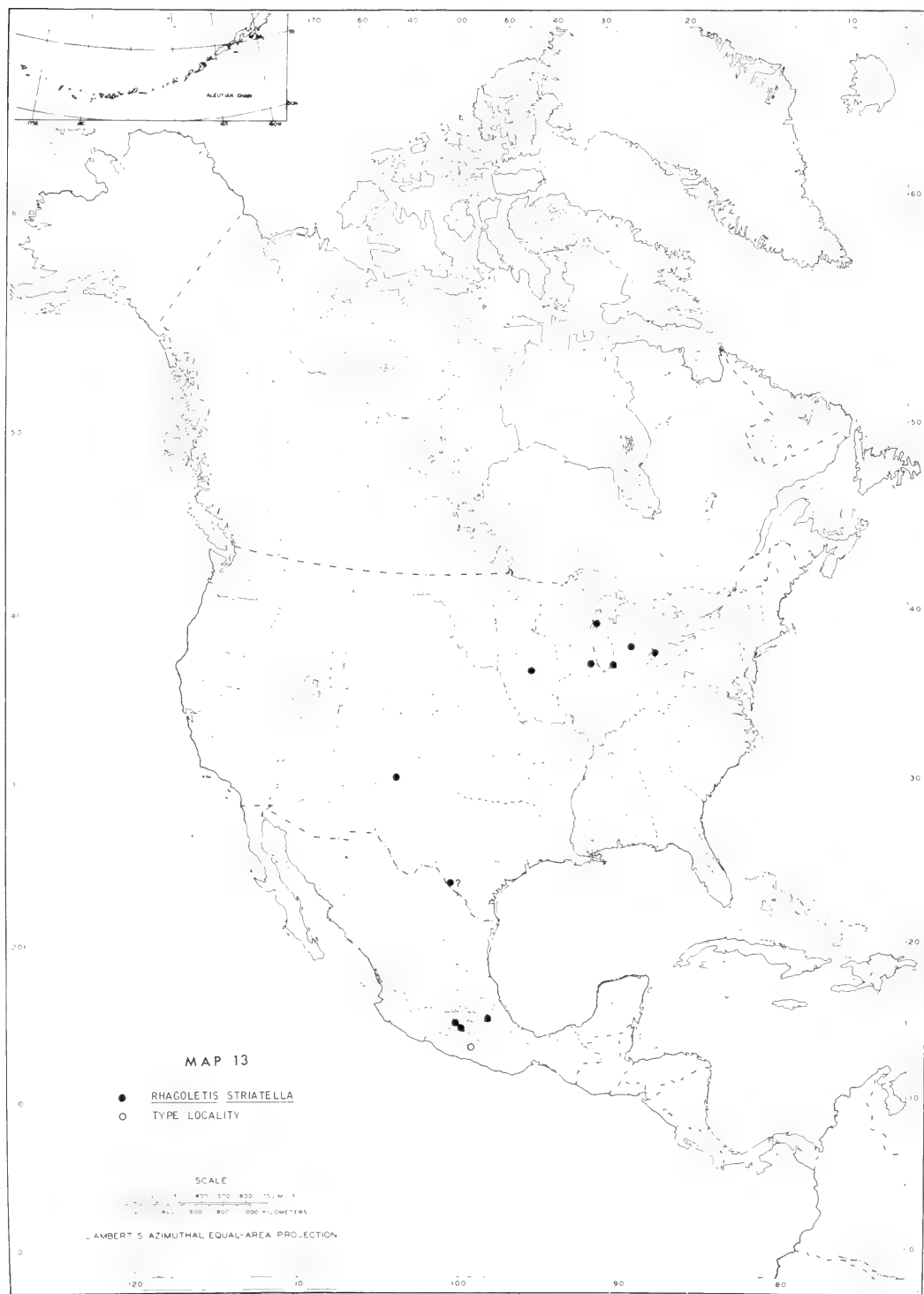
Distribution (Map 13). **CANADA:** ONTARIO: Chatham. **U.S.A.:** MICHIGAN: Agr. Coll. Mich., East Lansing, Ingham Co. WISCONSIN: Deer Co. ILLINOIS: Algonquin, McHenry Co. IOWA: vicinity of Gilbert, Story Co. NEW MEXICO: Las Vegas, San Miguel Co. TEXAS: Eagle Pass, Maverick Co. **MEXICO:** TLAXCALA: Huamantla. MEXICO: vicinity of Agua Bendita; Tenango de Valle; El Yukon. GUERRERO: Amulango (formerly Amula).

Rhagoletis fausta (Osten Sacken)

Trypeta (Acidia) fausta Osten Sacken, 1877, U.S. Geol. and Geogr. Survey Bull., 3: 346. [Syntypes examined: ♀, lectotype by present designation, Mt. Washington, N.H., Alpine No. 1332 (Geo. Dimmock) (Osten Sacken Coll.; MCZ, No. 10234); ♀, same locality and collector as lectotype, Alpine No. 1331.][19]

Rhagoletis fausta, —Coquillett, 1899, J. New York Ent. Soc., 7: 260 (syn. *Acidia fausta*). —Aldrich, 1910, Canad. Ent., 42: 99–100 (synonymizes *intrudens* with *fausta*). —Bezzi, 1911, Boll. Lab. Zool. Portici, 5: 19 (note, in key). —Phillips, 1923, J. New York Ent. Soc., 31: 135–136, pl. 28, fig. 26 (in key, note). —Cresson, 1929, Trans. Amer. Ent. Soc., 55: 404–405, pl. 14, fig. 2 (in key, redescription). —Curran, 1932, Amer. Mus. Nov., 526: 6 (in key). —Pickett, 1937, Canad. J. Res. (D), 15: 61 (genitalia). —Phillips, 1946, Mem. Amer. Ent. Soc., 12: 66, figs. 23, 68, 125, 126, 170 (larval morphology, in key).

Rhagoletis intrudens Aldrich, 1909, Canad. Ent., 41: 70, 72, pl. 4, fig. 3. [Type examined: ♀, Victoria, B.C., 6.3142, W. R. Palmer, emerged at Ottawa, 19.VI.1907 (USNM, No. 42214).]

There are two allopatric populations of *fausta* in North America (Map 14). No morphological differences could be found between these two populations which are confined to the northeastern and northwestern regions of the continent. In the absence of crossbreeding experiments, it is best to consider the two populations as

one species although they utilize different species of *Prunus* as hosts.

Diagnosis. R. fausta is easily distinguished from all other *Rhagoletis* by its characteristic wing pattern (Fig. 210) and the absence of white bands along the posterior margin of the abdominal tergites.

The only species with which *fausta* bears some resemblance is the female of the European leafminer, *Philophylla heraclei* Linnaeus, which has a similar wing pattern and general habitus. The position of crossvein r-m, the absence of a hyaline spot in cell R_3, black markings on the posterior region of head and legs, as well as the white scutellar spot, will easily distinguish *fausta* from *heraclei*. The male of *P. heraclei* is almost entirely yellow and resembles the male of *fausta* only in wing pattern.

The exact relation of *fausta* to other members of the genus *Rhagoletis* is uncertain. The globular spermathecae and apical F-shaped pattern of the wing show some similarity to *striatella*. However, the wide distribution of *fausta* in the northern cold temperate region, and its limitation to higher altitudes as it moves southward, indicate that this species is probably not of tropical origin. Its relationships will therefore have to remain in doubt until both the Asiatic and Neotropical representatives of the genus are better known.

Description. Body and wing measurements in Tables 12A–12B. *Head* (Fig. 40): posterior surface black. Postorbital, upper one-third of occiput, frons, antennae, and palps golden yellow; face, genae, and anterior margin of postgenae yellow to whitish yellow; mentum black. Postocellar, gular, and genal bristles yellow; all other major bristles, including single postvertical and 7–14 postorbitals, black; occasional specimens with four pairs of lower fronto-orbital bristles. *Thorax*: black except for yellowish white concolorous scutellum and notopleural stripe, latter with black shading only along lateral margins near base; postscutellum brownish black; halteres lemon

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[19] Osten Sacken's original description refers to a male and a female as cotypes. Both specimens bearing type labels in the MCZ collection are females.

yellow. Dorsum covered with brownish black decumbent setae and diffuse white pollinose microtrichia arranged in four ill-defined broad rows; in some specimens medial rows more distinct than outer rows; dorsocentrals slightly before anterior supra-alars; one well developed mesopleural with smaller, lower bristle present in most specimens; pteropleural bristle reduced, sometimes minute, usually one-third length of upper mesopleural bristle. *Legs*: coxae and femora dark brownish black; trochanters, all tibiae, and tarsal segments yellow. Tibiae II and III may bear light to heavy brown shading, particularly on posterior surface. *Wing*: pattern as in Figure 210; R_{4+5} bare except for single seta on dorsal surface of junction with R_{2+3}. Medial band broadly joined to subapical band in cell 1st M_2; large hyaline spot in subapical band just apicad of junction; apical band forked, similar to that of *striatella*. Crossvein r-m about midway between m and M_3. Anal cell pointed. *Abdomen*: all segments in both sexes entirely black, without white band along posterior margin. *Genitalia*: *male*—epandrium black, surstyli yellowish orange (Figs. 74, 110); phallic apodeme curved; genital ring membrane normal. Aedeagus (Fig. 117) without apical appendage; vesica smooth. Ejaculatory apodeme normal (Fig. 151). *Female*—variation in ovipositor length shown in Figure 19; ovipositor tip with two minute subapical setae; ovipositor sheath black. Three spermathecal ducts, two globular spermathecae (Fig. 171) covered with appressed scale-like papillae.

Chromosome number and morphology (Figs. 236–237). The diploid number in both sexes is 12; the MCA number is 22 as there are five pairs of metakinetic chromosomes and a single pair of acrokinetic dot chromosomes. At metaphase, a secondary constriction is sometimes present on one pair of submetakinetic chromosomes (Fig. 236), and a distinct satellite is always clearly visible at metaphase in a second pair of submetakinetic chromosomes (Fig.

236). No morphologically differentiated heterochromosomes (XY) were observed.

Source of cytological material: *Prunus pennsylvanica,* Blue Hills, vicinity Canton, Mass., 300 ft., July 4, 1963. *P. emarginata,* Blue Canyon Airport, Placer Co., California, 5,200 ft., Aug. 9, 1961.

Courtship behavior. The courtship behavior of this species was not studied.

Parasites. Middlekauff (1941) and Frick et al. (1954) found the following hymenopterous parasites attacking *fausta: Pachycrepoideus dubius* Ashmead (Pteromalidae); *Tetrastachus faustus* Burks (Eulophidae); *Eucoilia* sp. (Cynipidae); *Phydgadeuon epochrae* Viereck (Ichneumonidae).

Hosts. Details of the host relationships of this species have been discussed by Frick et al. (1954). *R. fausta* was recorded infesting cultivated cherries in British Columbia by Aldrich (1909), who incorrectly named it *R. intrudens.* In 1910 he recognized his error and synonymized his own species with *fausta.* Soon afterward, Illingworth (1912) reported that *fausta* was also a pest of cultivated sour cherries (*Prunus cerasus* L.) in New York, and similar records followed from other eastern localities. The first native hosts of *fausta* were not reported until 1918 when Severin found the pin, or fire cherry (*Prunus pennsylvanica* L. f.), to be infested exclusively with this species. Farleman (1932) also reared *fausta* from the fruits of *P. serotina* Ehrh., *P. virginiana* L., and *P. mahaleb* L., while Glasgow (1933) found *P. pennsylvanica* to be the preferred host of this species, although he was able to rear a few individuals from *P. virginiana* and *P. mahaleb.* Mackie (1940) recorded the western population of *fausta* infesting the fruits of *P. emarginata* (Dougl.) D. Dietr. With the possible exception of the isolated population of *P. emarginata* in Arizona, *fausta* probably infests the fruits of this plant over most of its range in western North America.

In the West, *fausta* does not effectively compete with *indifferens* when both occur in the same locality. Frick et al. (1954)

MAP 14

- ● RHAGOLETIS FALSTA
- ○ LOCALITIES CITED IN LITERATURE
- ——— PRUNUS EMARGINATA
- —·—·— PRUNUS VIRGINIANA (ARROW)
- ············ PRUNUS PENNSYLVANICA

SCALE

LAMBERTS AZIMUTHAL EQUAL AREA PROJECTION
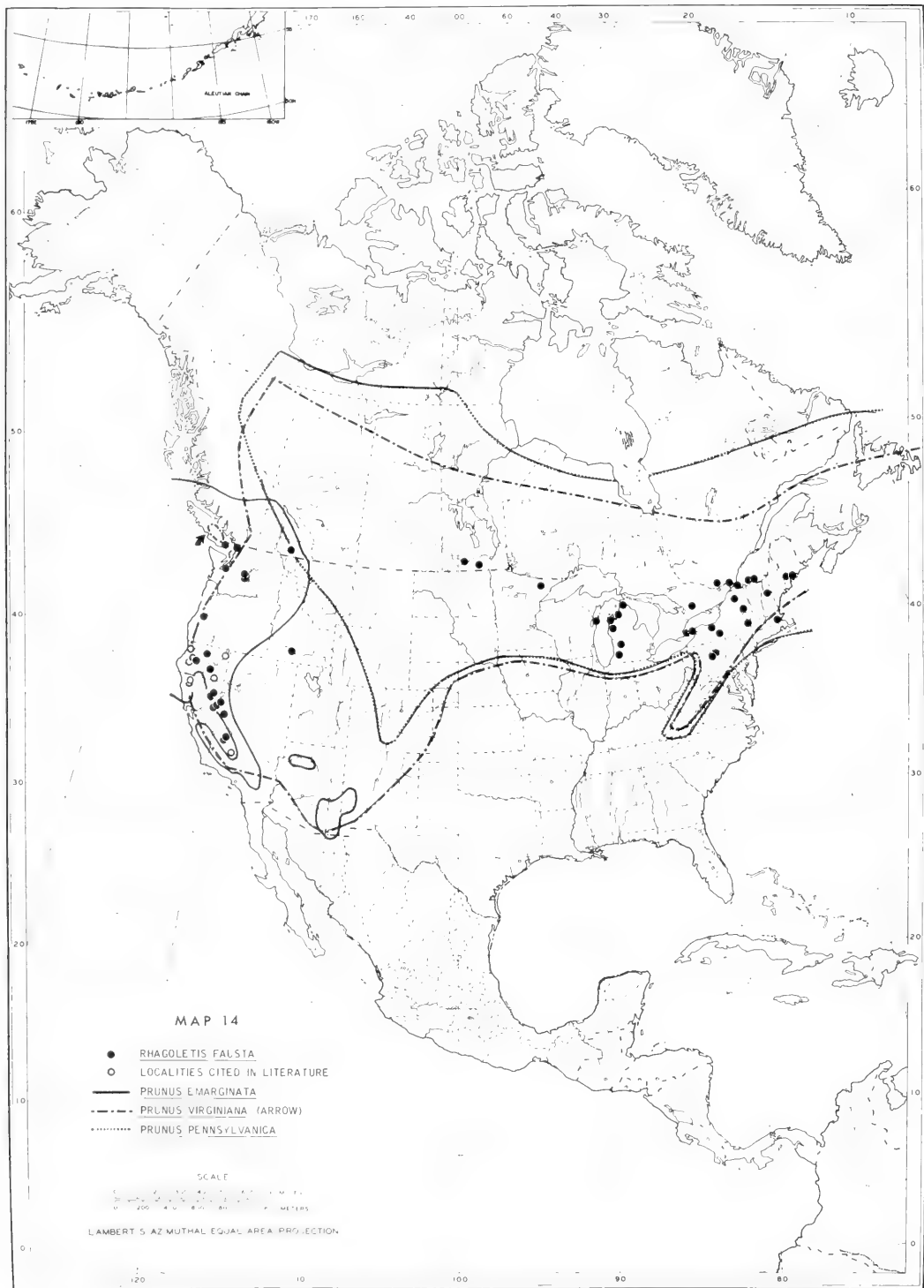
found that of 995 pupae sifted from soil under a *P. emarginata* tree, only four were *fausta*. The black cherry fruit fly in most areas emerges and is most active approximately one to three weeks before *cingulata*. The only known exception is the Vancouver Island population which emerges from two weeks to a month later than *cingulata* (Raine and Andison, 1958). In California, *fausta* is usually found at higher altitudes than *indifferens* (Wasbauer and Blanc, 1962, personal communication). This fact, along with the difference in emergence periods, may act to reduce competition between *fausta* and *indifferens*.

Distribution (Map 14). Neither eastern nor western populations of *R. fausta* extend as far north or south as their host plants. The eastern population, following the pattern common to many other *Rhagoletis* species, does not extend westward beyond the 100th meridian.

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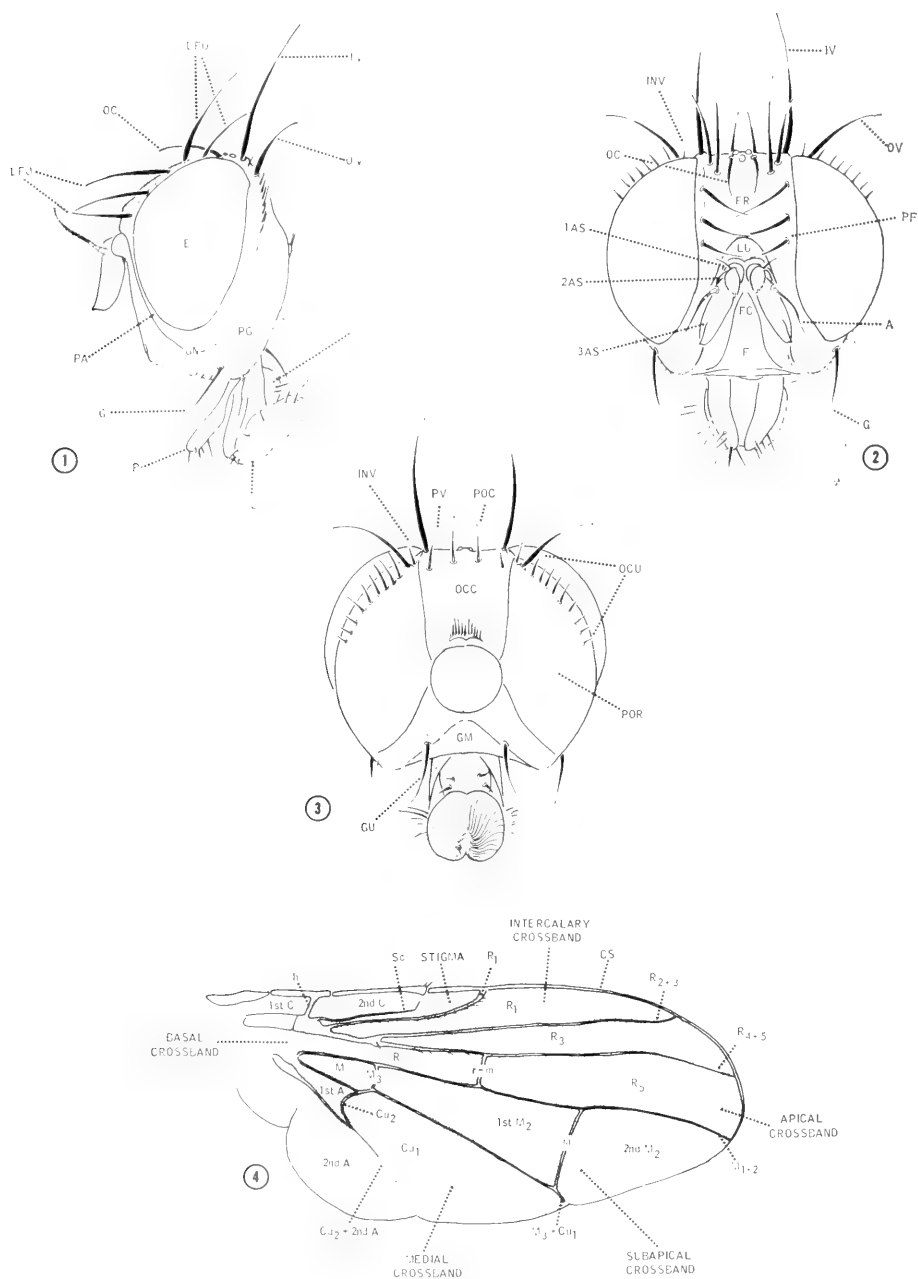
Figures 1-3. Chaetotaxy and areas of the head. Fig. 1, side view. Fig. 2, front view. Fig. 3, posterior view. Abbreviations: A, arista; E, eye; F, face; FC, facial carina; FR, frontalia; G, genal bristle; GM, gulamentum; GN, gena; GU, gular bristle; INV, intravertical bristle; IV, innervertical bristle; L, labella; LFO, lower fronto-orbital bristles; LU, lunule; M, mentum; OC, ocellar bristle; OCC, occiput; OCU, postocellar bristles; OV, outervertical bristle; P, palpi; PA, parafacial; PF, parafrontal; PG, postgenae; POC, postvertical bristle; POR, postorbital region; PV, postvertical bristle; UFO, upper fronto-orbital bristles; 1AS, first antennal segment; 2AS, second antennal segment; 3AS, third antennal segment.

Figure 4. Wing showing cells, venation, and generalized wing pattern.
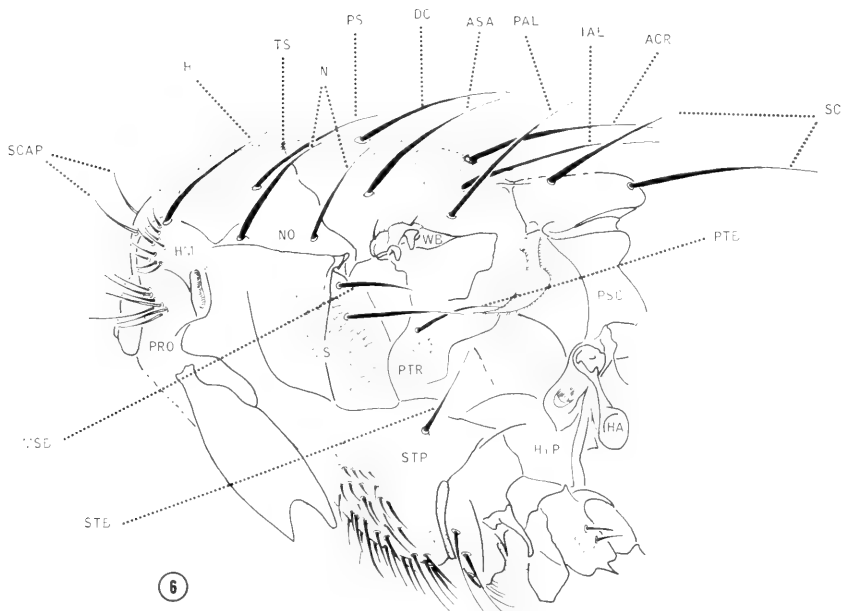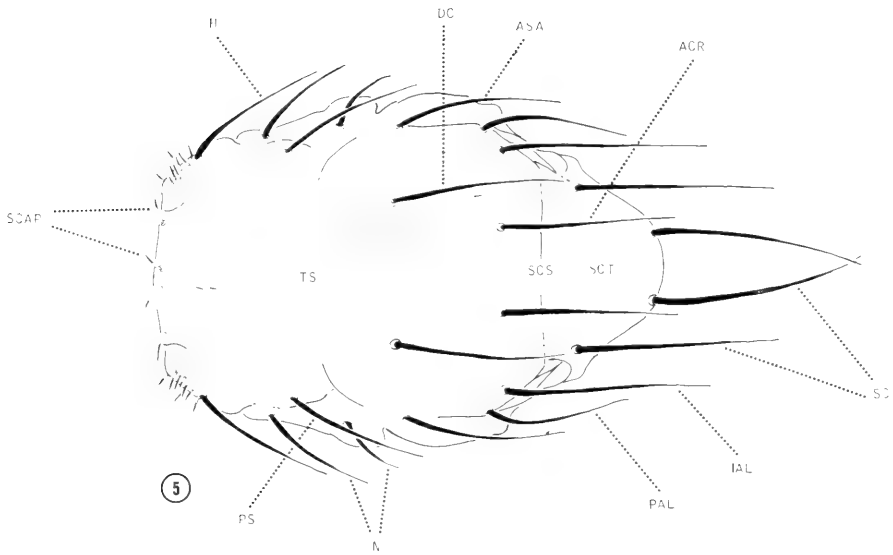
Figures 5–6. Chaetotaxy and areas of the thorax. Fig. 5, dorsal view. Fig. 6, side view. Abbreviations: ACR, acrostichal bristle; ASA, anterior supraalar; DC, dorsocentral bristle; H, humeral bristle; HA, haltere; HM, humerus; HYP, hypopleuron; IAL, intraalar bristle; MS, mesopleuron; MSB, mesopleural bristle; N, notopleural bristle; NO, notopleuron; PAL, postalar bristle; PRO, propleuron; PS, presutural bristle; PSC, postscutellum; PTB, pteropleural bristle; PTR, pteropleuron; SC, scutellar bristle; SCAP, scapular bristle; SCS, scutoscutellar suture; SCT, scutellum; STB, sternopleural bristle; STP, sterno-pleuron; TS, transverse suture; WB, wing base.

COXA I

FEMUR I

TIBIA I

⑦

PROTHORACIC LEG, POSTERIOR VIEW

TARSUS I

FEMUR II

TIBIA II

TARSUS II

COXA II

⑧

MESOTHORACIC LEG, ANTERIOR VIEW

TIBIA III

FEMUR III

⑨

COXA III

METATHORACIC LEG, ANTERIOR VIEW

TARSUS III
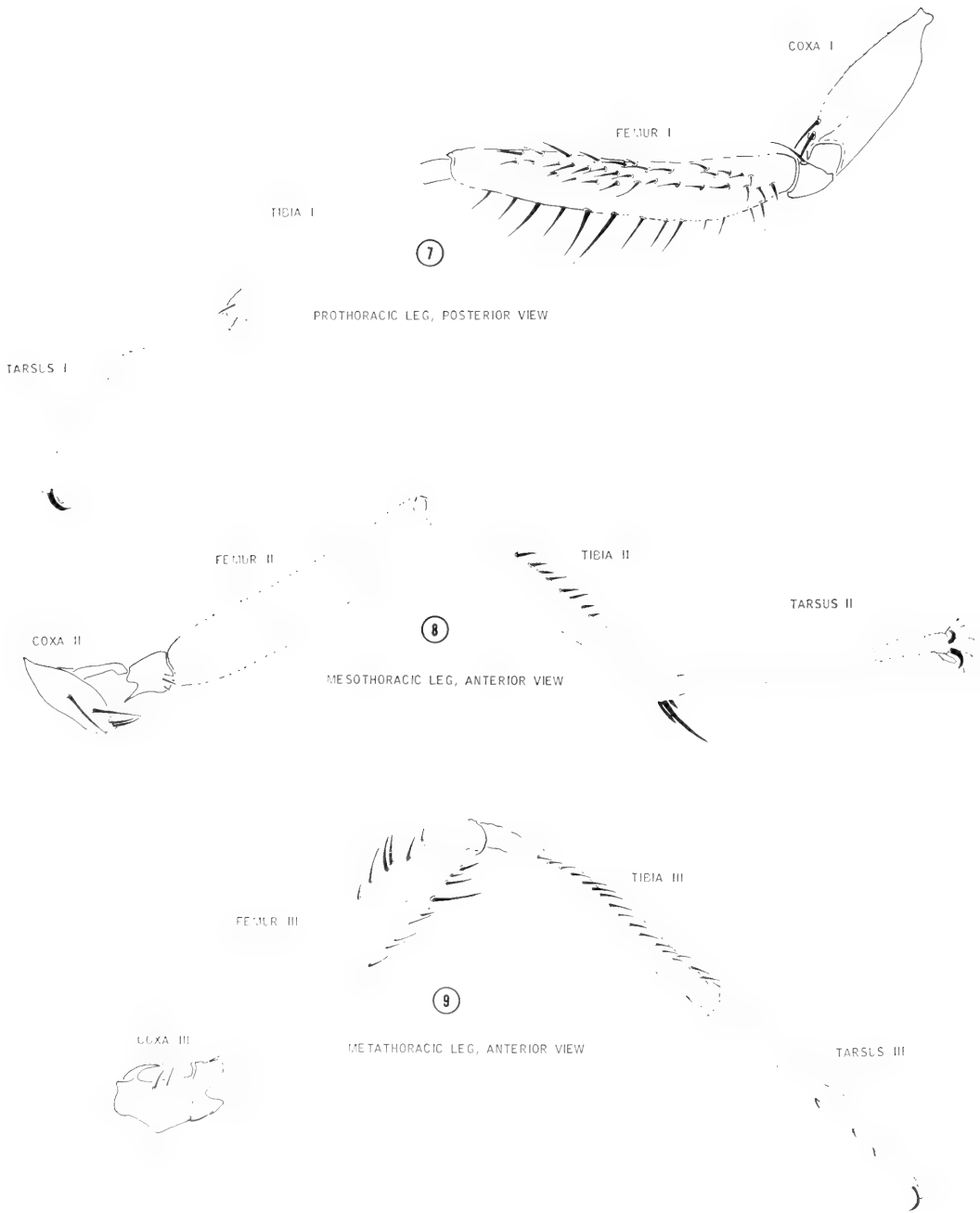
Figures 7–9. Legs showing arrangement of major bristles. Fig. 7. Prothoracic leg, posterior view. Fig. 8. Mesothoracic leg, anterior view. Fig. 9. Metathoracic leg, anterior view.
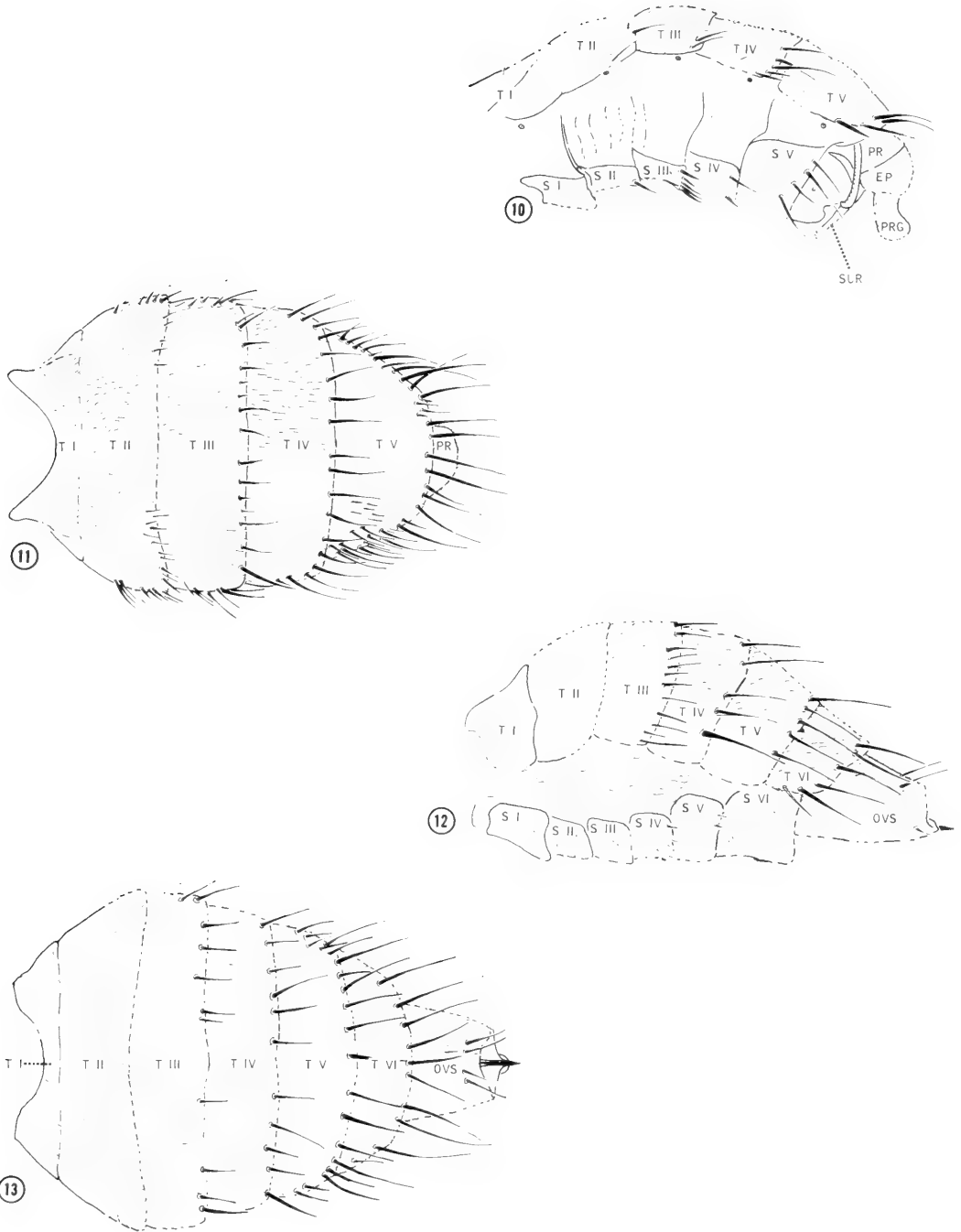
Figures 10–13.   Abdomen showing segmentation and position of bristles. Fig. 10, ♂, lateral view. Fig. 11, ♂, dorsal view. Fig. 12, ♀, lateral view. Fig. 13, ♀, dorsal view. Abbreviations: EP, epandrium; OVS, ovipositor sheath; PR, protandrium; PRG, proctiger; SUR, surstyli; T, tergites; S, sternites.
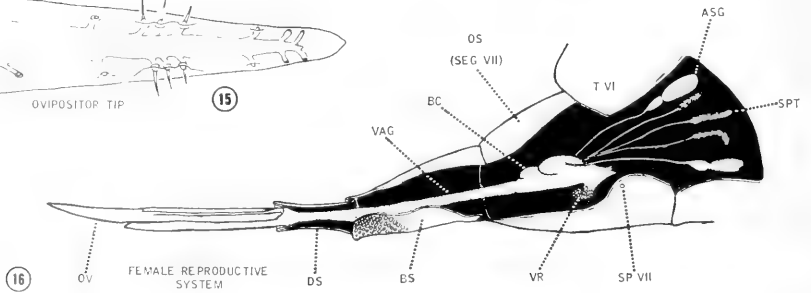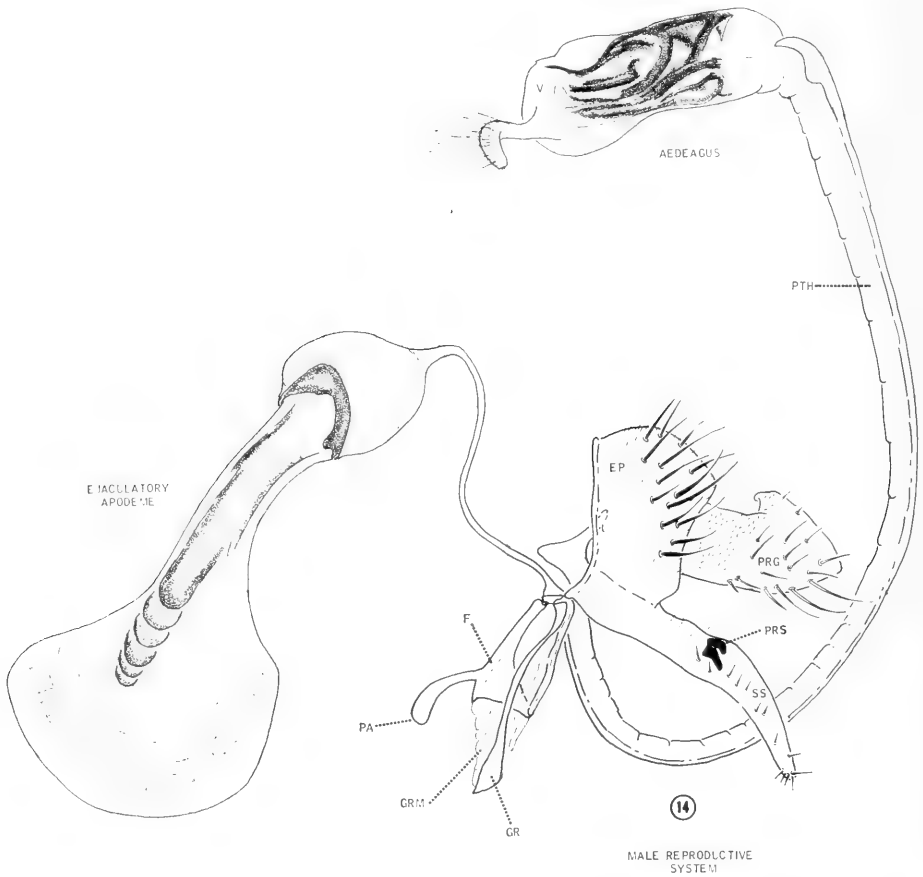
Figure 14.   Terminalia of male: EP, epandrium; F, fultella; GR, genital ring; GRM, genital ring membrane; PA, phallic apodeme; PRG, proctiger; PRS, prensisetae; PTH, phallotheca.

Figure 15.   Detail of ovipositor tip showing three pairs of preapical setae.

Figure 16.   Sclerotized portion of female reproductive system: ASG, accessory gland; BC, bursa copulatrix; BS, basal sheath; DS, distal sheath; OS, ovipositor sheath; OV, ovipositor; SEG, segment; SP, spiracle; SPT, spermatheca; T, tergite; VAG, vagina; VR, ventral receptacle.
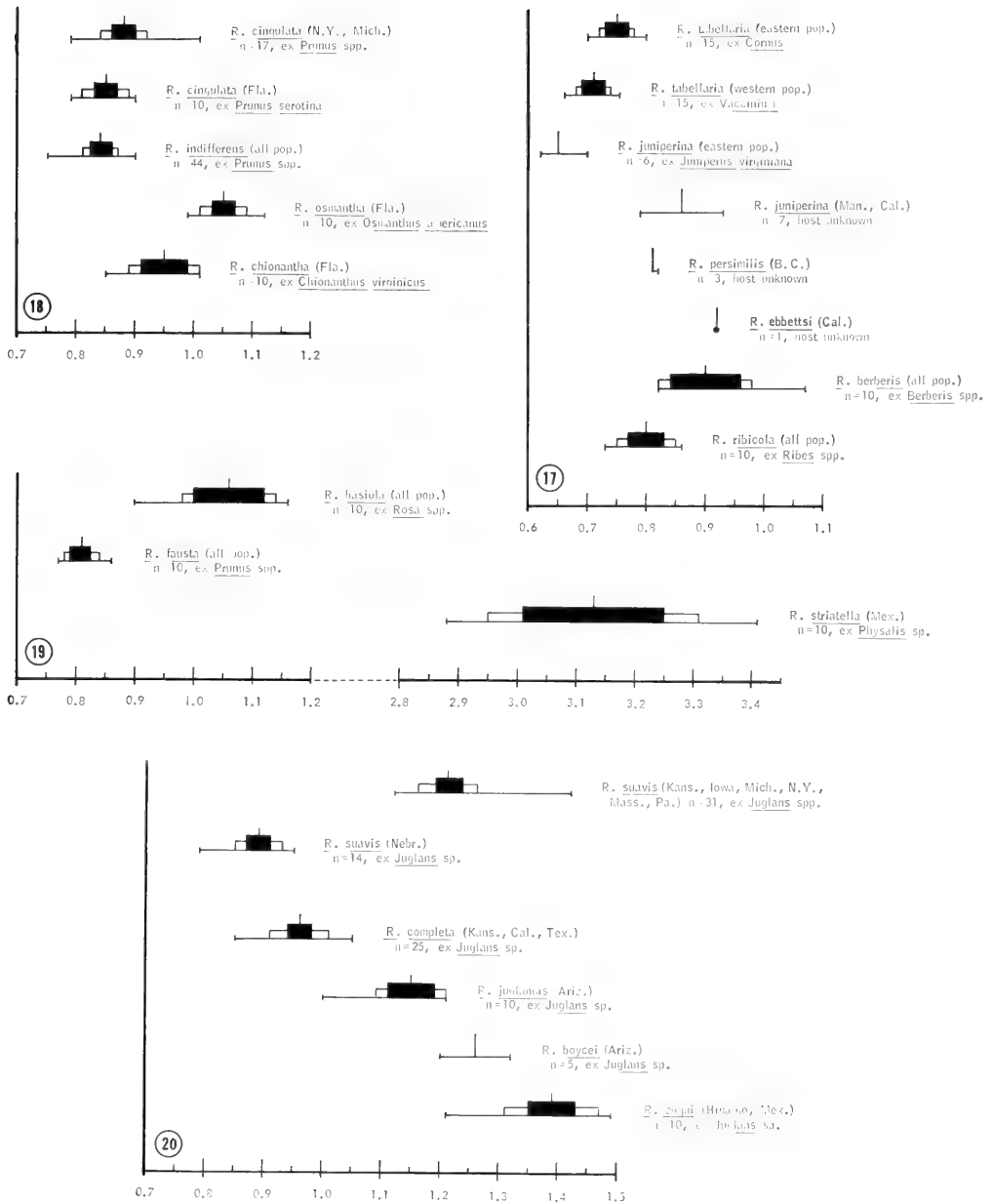
Figures 17–20. Dice-Leraas diagrams showing interspecific variation in ovipositor length. Horizontal lines represent observed ranges, rectangular mark standard deviation, and solid black indicates 95 per cent confidence intervals for the mean. Fig. 17. tabellaria species group. Fig. 18. cingulata species group. Fig. 19. Miscellaneous species. Fig. 20. suavis species group.
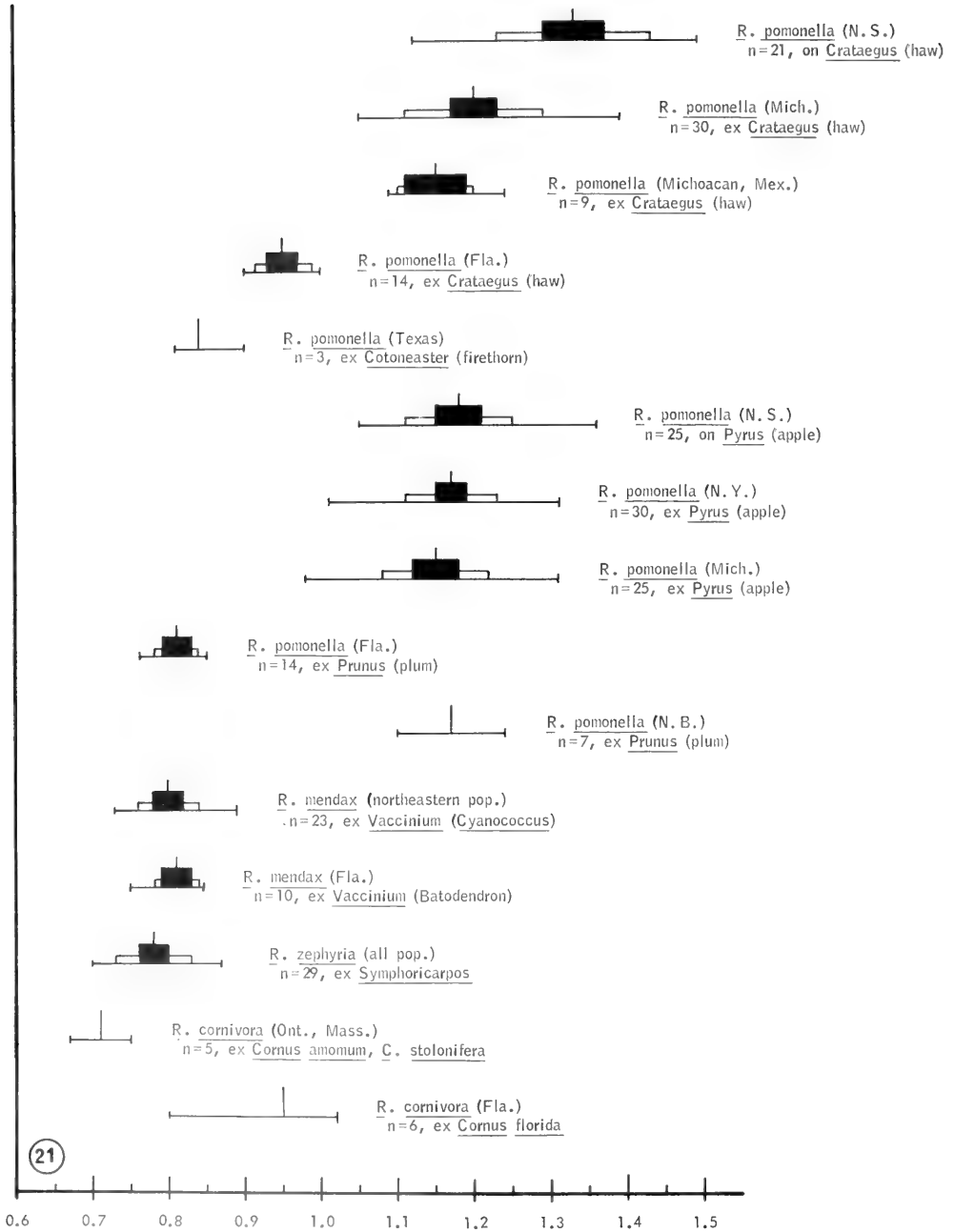
Figure 21. Dice-Leraas diagram showing interspecific variation in ovipositor length in species of the *pomonella* species group. Horizontal lines represent observed ranges, rectangular mark standard deviation, and solid black indicates 95 per cent confidence intervals for the mean.
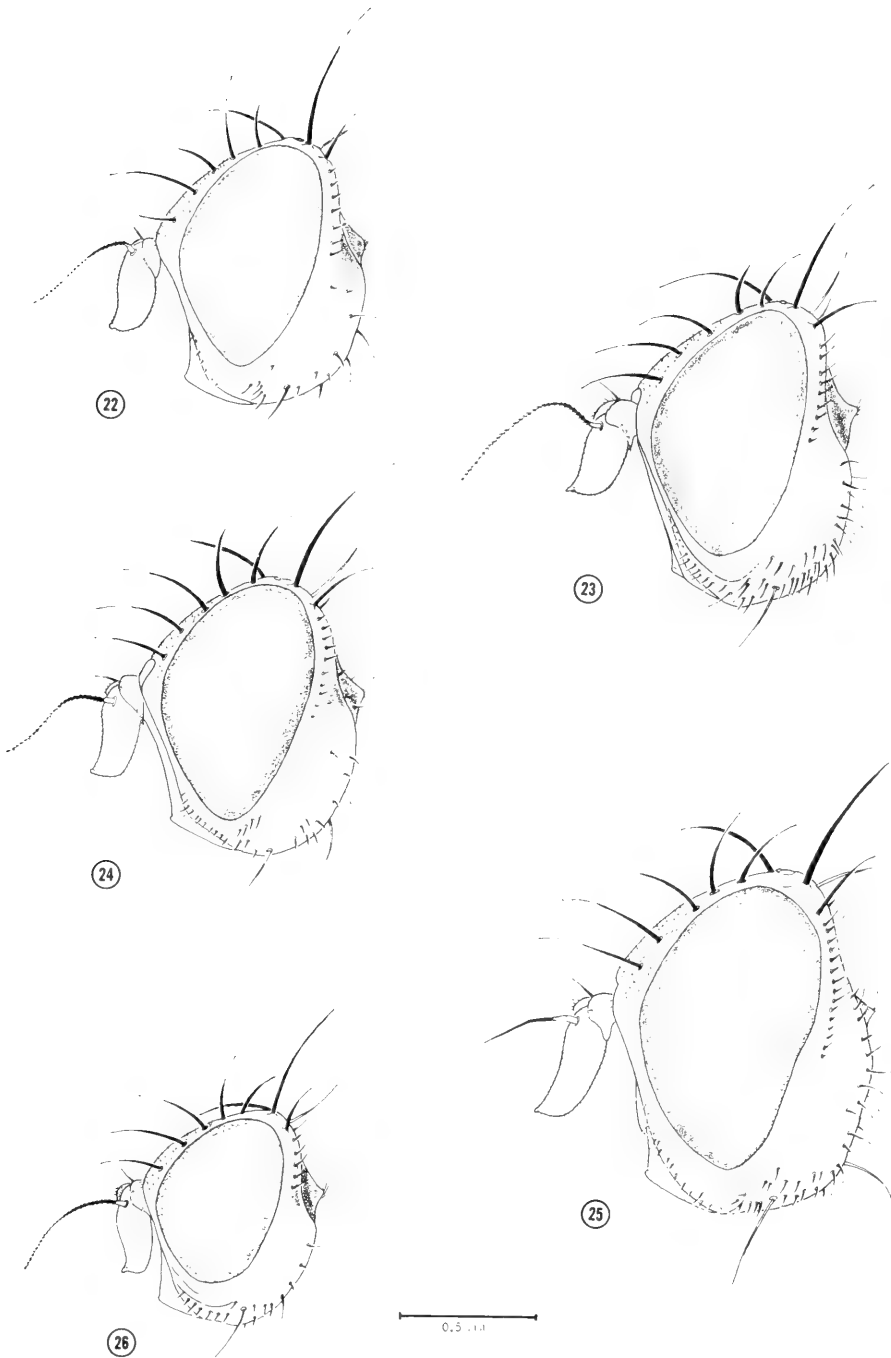
Figures 22–26. Lateral view of head of *Rhagoletis* species. Fig. 22. *R. zephyria* Snow, ♂, Calif. Fig. 23. *R. cornivora* n. sp., ♂, Mass. Fig. 24. *R. mendax* Curran, ♂, Maine. Fig. 25. *R. pomonella* (Walsh), ♂, Mass. Fig. 26. *R. mendax* Curran, ♂, Fla.
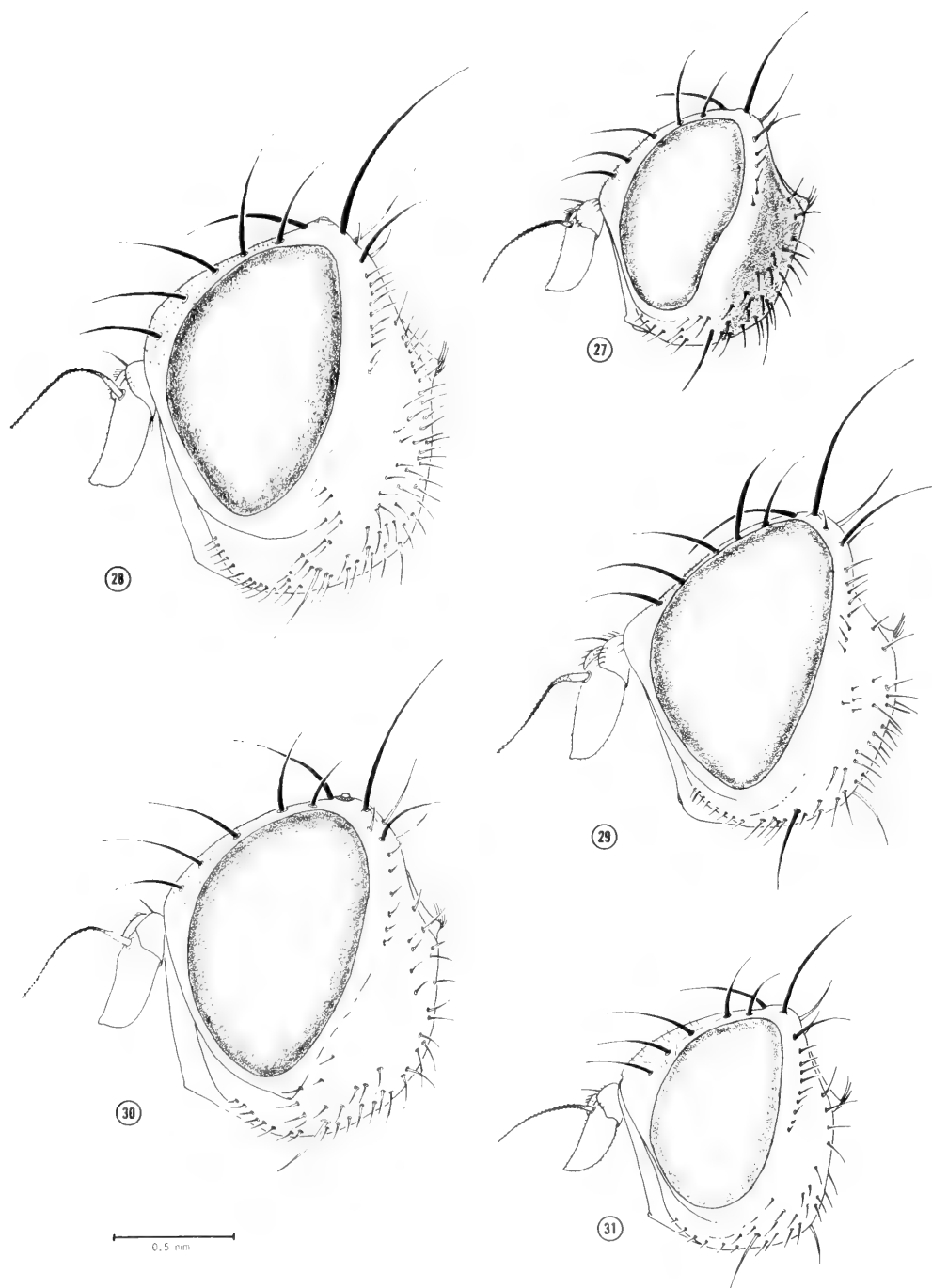
Figures 27–31. Lateral view of head of *Rhagoletis* species. Fig. 27. *R. boycei* Cresson, ♂, Ariz. Fig. 28. *R. completa* Cresson, ♂, Calif. Fig. 29. *R. zoqui* n. sp., ♂, Hidalgo, Mex. Fig. 30. *R. suavis* (Loew), ♂, Mass. Fig. 31. *R. juglandis* Cresson, ♂, Ariz.
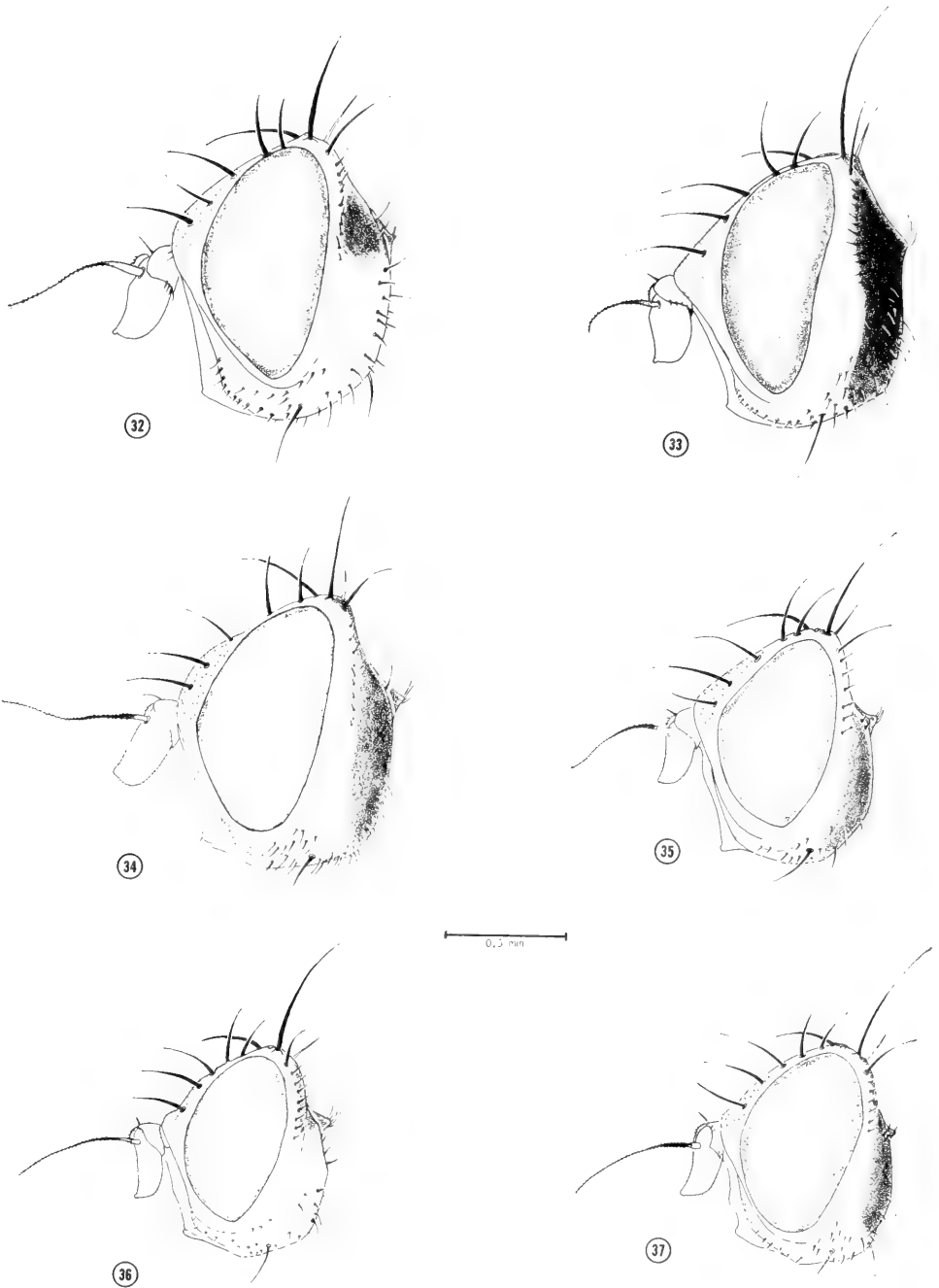
Figures 32–37. Lateral view of head of *Rhagoletis* species. Fig. 32. *R. cingulata* (Loew), ♂, Mass. (also typical of *indifferens, osmanthi* and *chionanthi*). Fig. 33. *R. persimilis* n. sp., ♂, B.C., Can. Fig. 34. *R. tabellaria* (Fitch), ♂, Mass. Fig. 35. *R. berberis* Curran, ♂, Ore. Fig. 36. *R. juniperina* Marcovitch, ♂, Mass. Fig. 37. *R. ribicola* Doane, ♂, Ore.
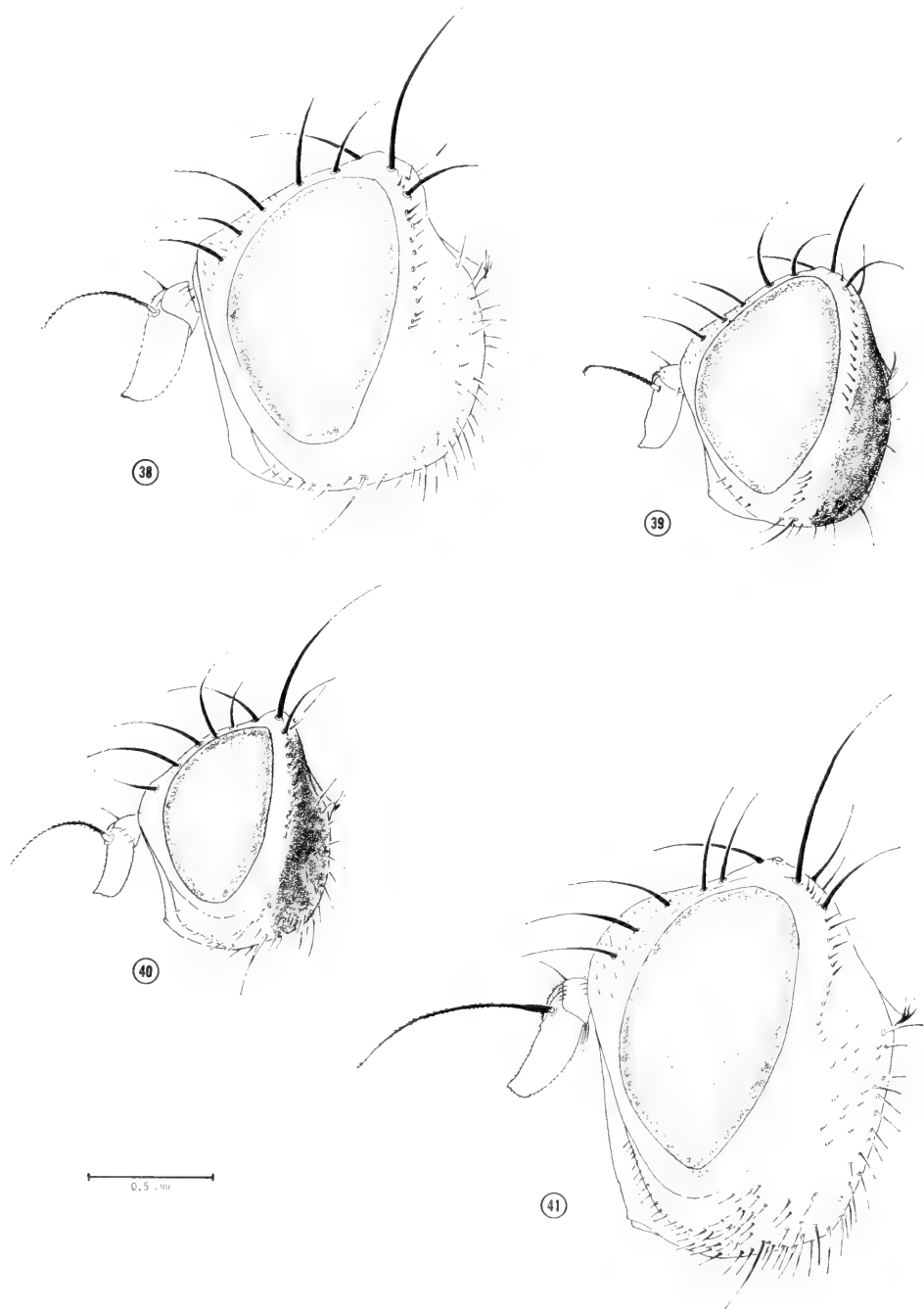
Figures 38–41. Lateral view of head of *Rhagoletis* species. Fɪg. 38. *R. basiola* (Osten Sacken), ♂ , Mass. Fig. 39. *R. cerasi* (Linn.), ♀ , France. Fig. 40. *R. fausta* (Osten Sacken), ♂ , N.H. Fɪg. 41. *R. striatella* van der Wulp, ♂ , Mexico.
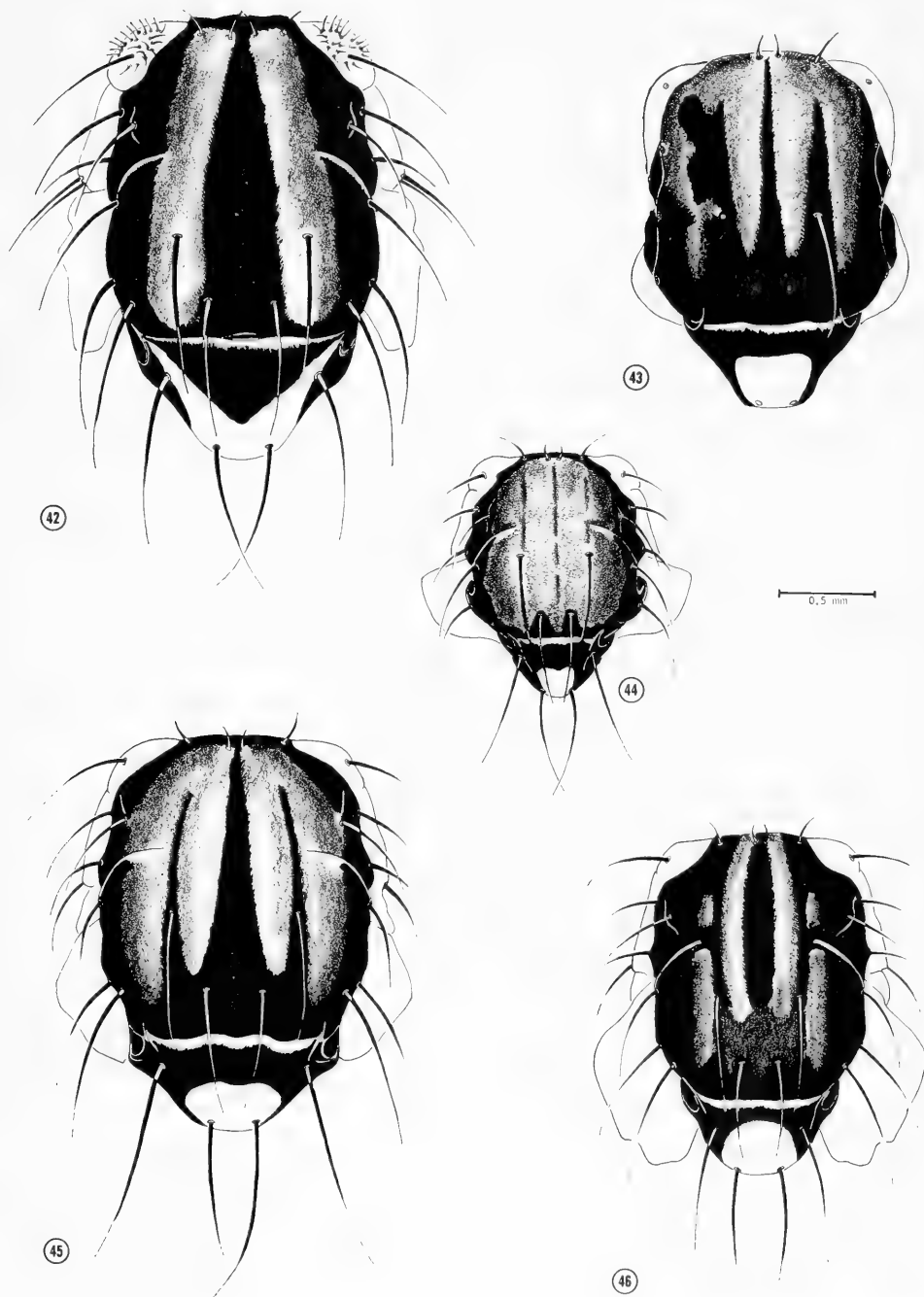
Figures 42–46. Dorsal view of thorax of *Rhagoletis* species. Fig. 42. *R. striatella* van der Wulp, ♂, Mexico. Fig. 43. *R. ebbettsi* n. sp., ♀ (holotype), Calif. Fig. 44. *R. juniperina* Marcovitch, ♂, Mass. Fig. 45. *R. pomonella* (Walsh), ♂, Mass. Fig. 46. *R. tabellaria* (Fitch), ♂, Mass. (also typical of *persimilis*, *ribicola* and *berberis*).
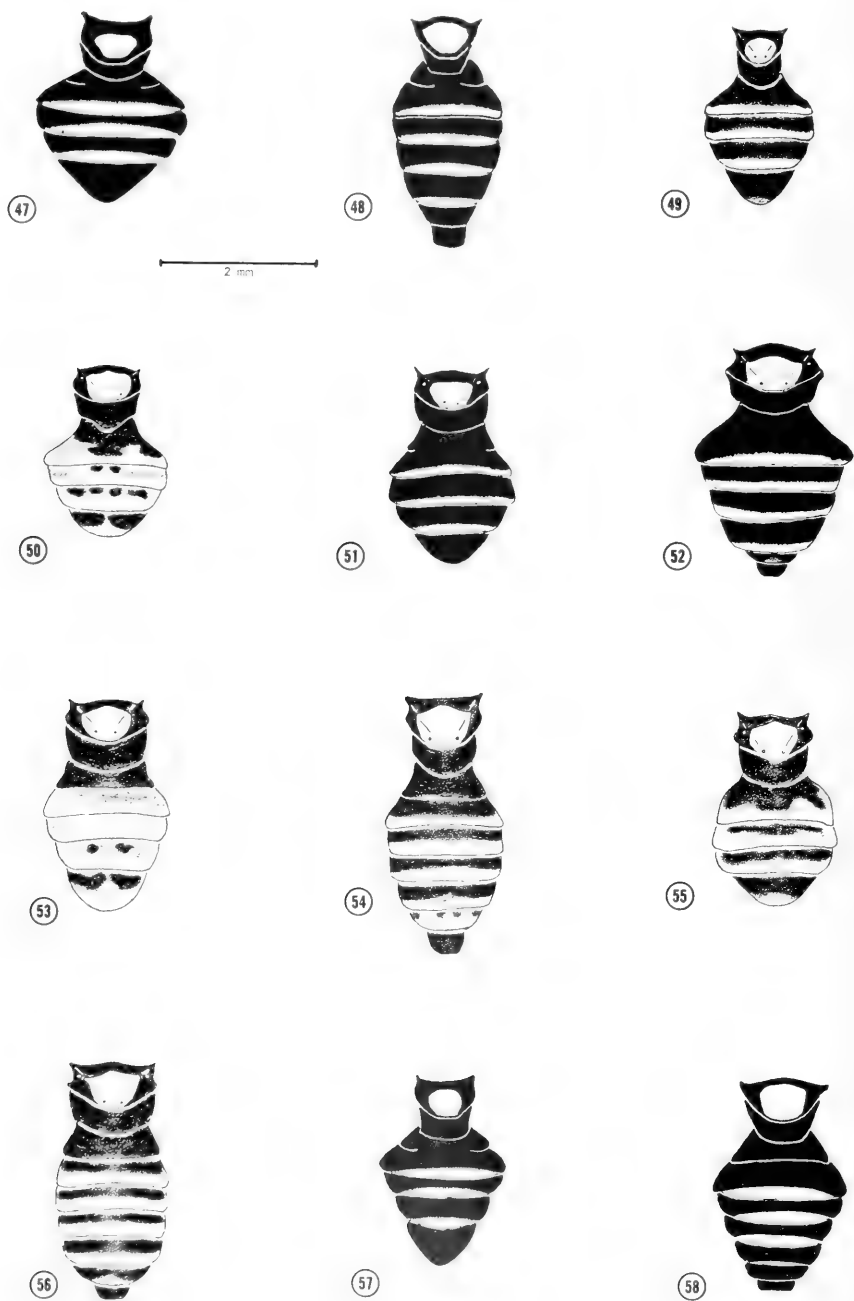
Figures 47–58. Dorsal view of abdomen of *Rhagoletis* species. Fig. 47. *R. pomonella* (Walsh), ♂, Mass. Fig. 48. *R. pomonella* (Walsh), ♀, Mass. Fig. 49. *R. cingulata* (Loew), ♂, N.Y. Fig. 50. *R. cingulata* (Loew), ♂, Fla. Fig. 51. *R. indifferens* Curran, ♂, Ore. Fig. 52. *R. indifferens* Curran, ♀, Ore. Fig. 53. *R. osmanthi* n. sp., ♂, Fla. Fig. 54. *R. osmanthi* n. sp., ♀, Fla. Fig. 55. *R. chionanthi* n. sp., ♂, Fla. Fig. 56. *R. chionanthi* n. sp., ♀, Fla. Fig. 57. *R. tabellaria* (Fitch), ♂, Wash. (also typical of *juniperina, persimilis, ribicola* and *berberis*). Fig. 58. *R. tabellaria* (Fitch), ♀, Wash. (also typical of *juniperina, persimilis, ebbettsi, ribicola* and *berberis*).
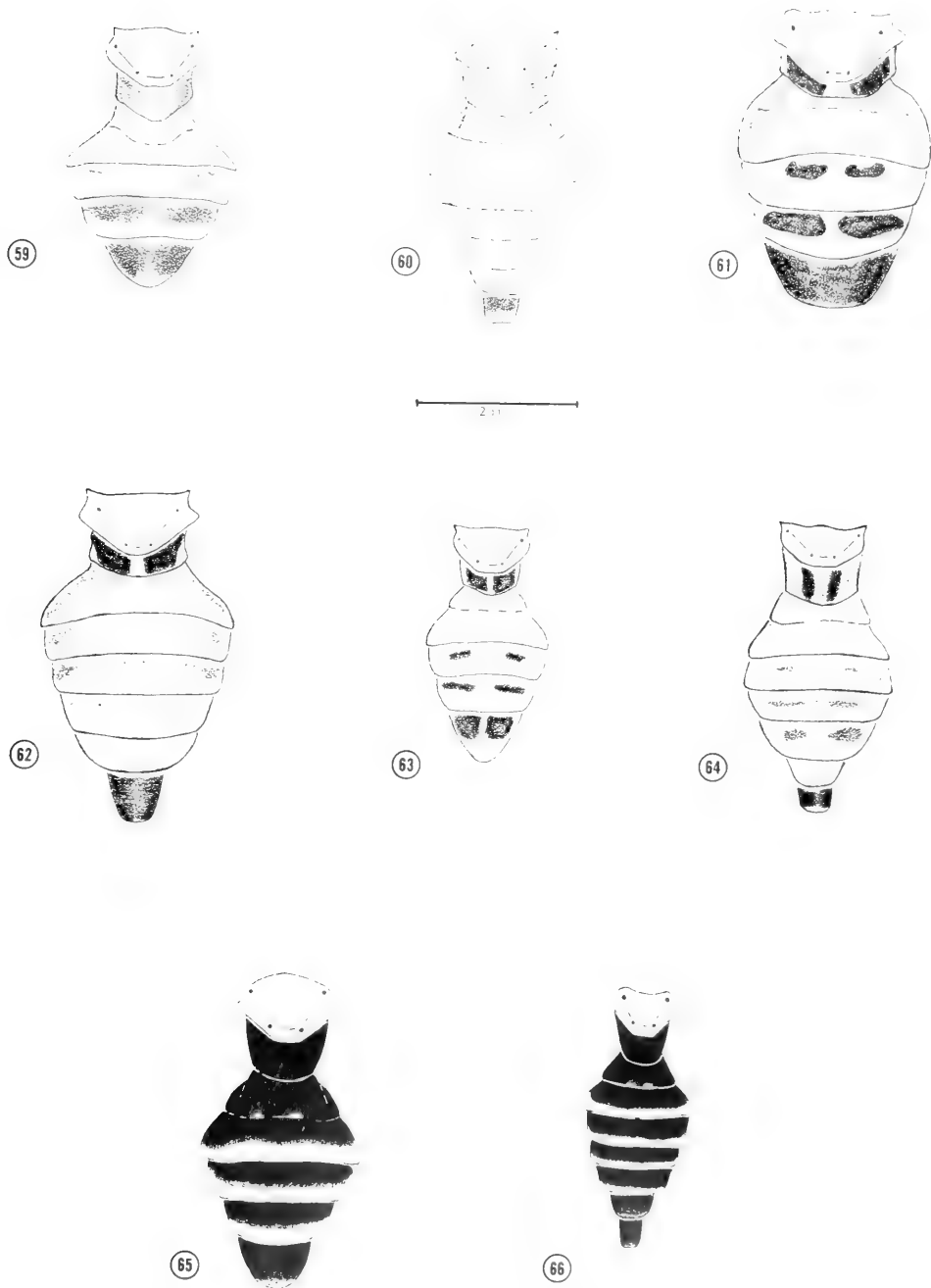
Figures 59–66. Dorsal view of abdomen of *Rhagoletis* species. Fig. 59. *R. suavis* Loew, ♂, Mass. Fig. 60. *R. suavis* (Loew), ♀, Mass. Fig. 61. *R. zoqui* n. sp., ♂, Hidalgo, Mex. Fig. 62. *R. zoqui* n. sp., ♀, Hidalgo, Mex. Fig. 63. *R. completa* Cresson, ♂, Calif. Fig. 64. *R. completa* Cresson, ♀, Calif. Fig. 65. *R. boycei* Cresson, ♂, Ariz. Fig. 66. *R. boycei* Cresson, ♀, Ariz.
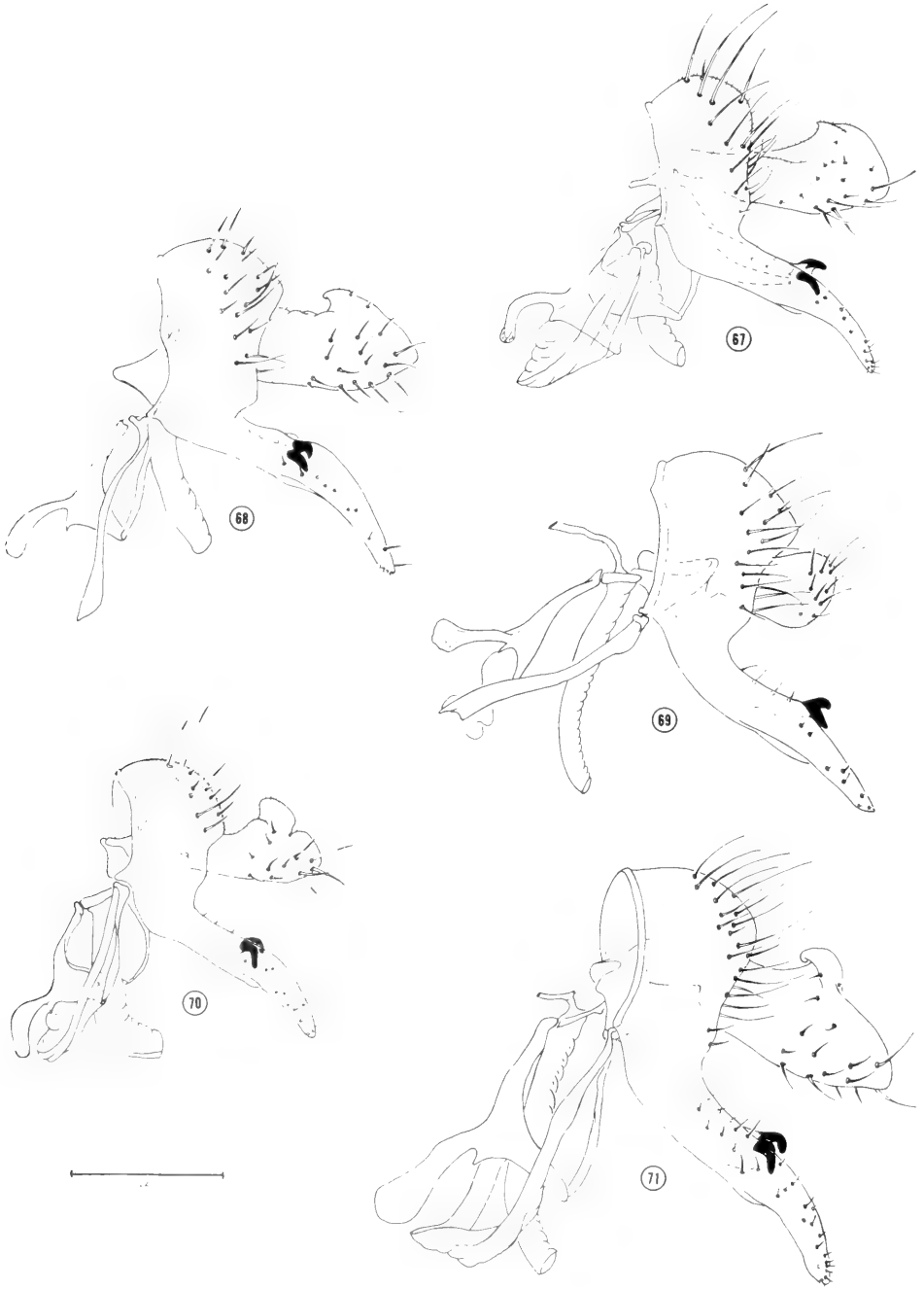
Figures 67–71. Lateral view of male genitalia of *Rhagoletis* species. Fig. 67. *R. mendax* Curran, Maine. Fig. 68. *R. cornivora* n. sp., Mass. Fig. 69. *R. zephyria* Snow, Ore. Fig. 70. *R. mendax* Curran, Fla. Fig. 71. *R. pomonella* (Walsh), Mass.
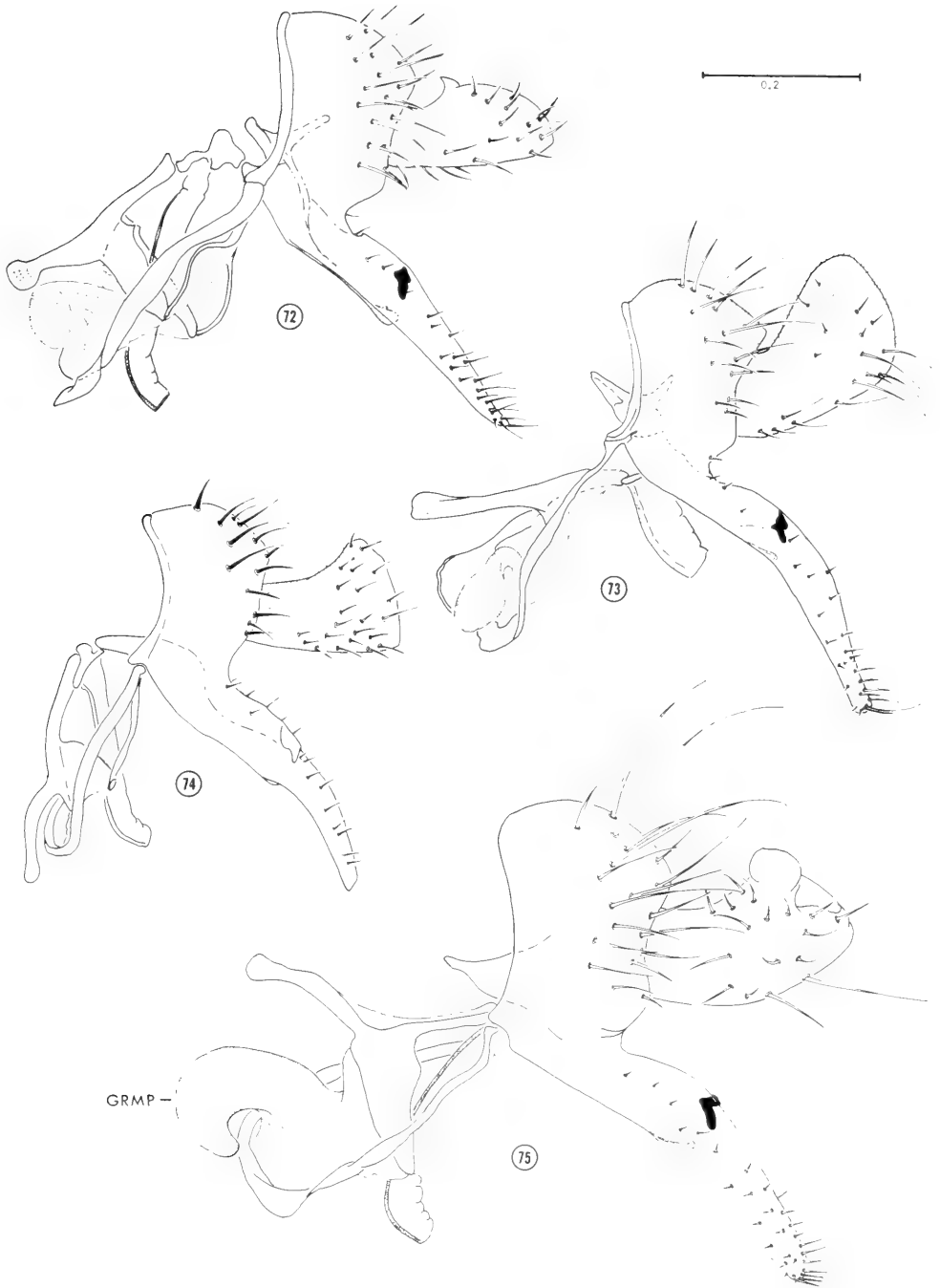
Figures 72–75. Lateral view of male genitalia of *Rhagoletis* species. Fig. 72. *R. juglandis* Cresson, Ariz. Fig. 73. *R. completa* Cresson, Calif. Fig. 74. *R. fausta* (Osten Sacken), N.H. Fig. 75. *R. suavis* (Loew), Mass. (GRMP, genital ring membrane pouch).
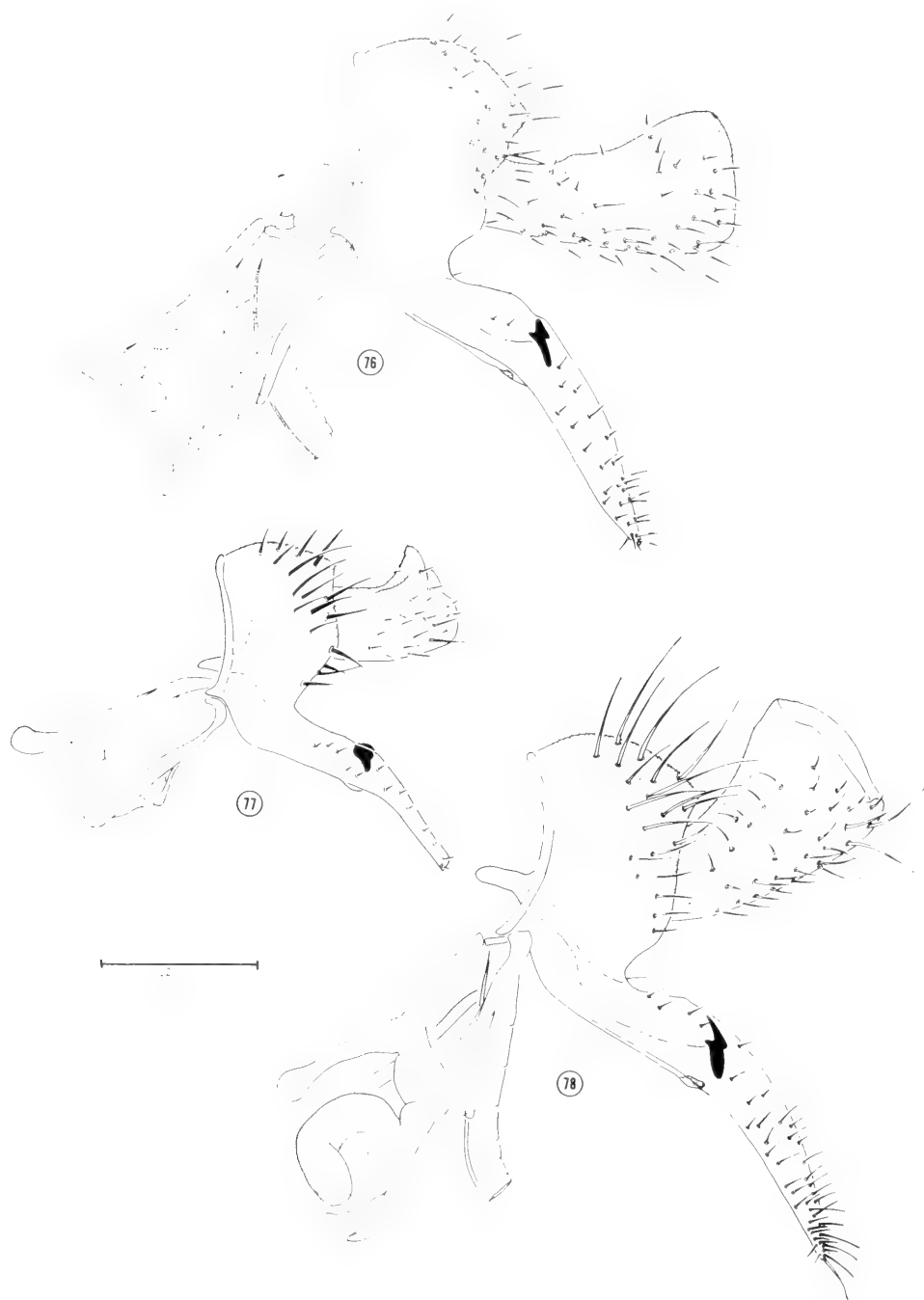
Figure 76-78. Lateral view of male genitalia of *Rhagoletis* species. Fig. 76. *R. boycei* Cresson, Ariz. Fig. 77. *R. cerasi* Linn., France. Fig. 78. *R. zoqui* n. sp., Hidalgo, Mex.
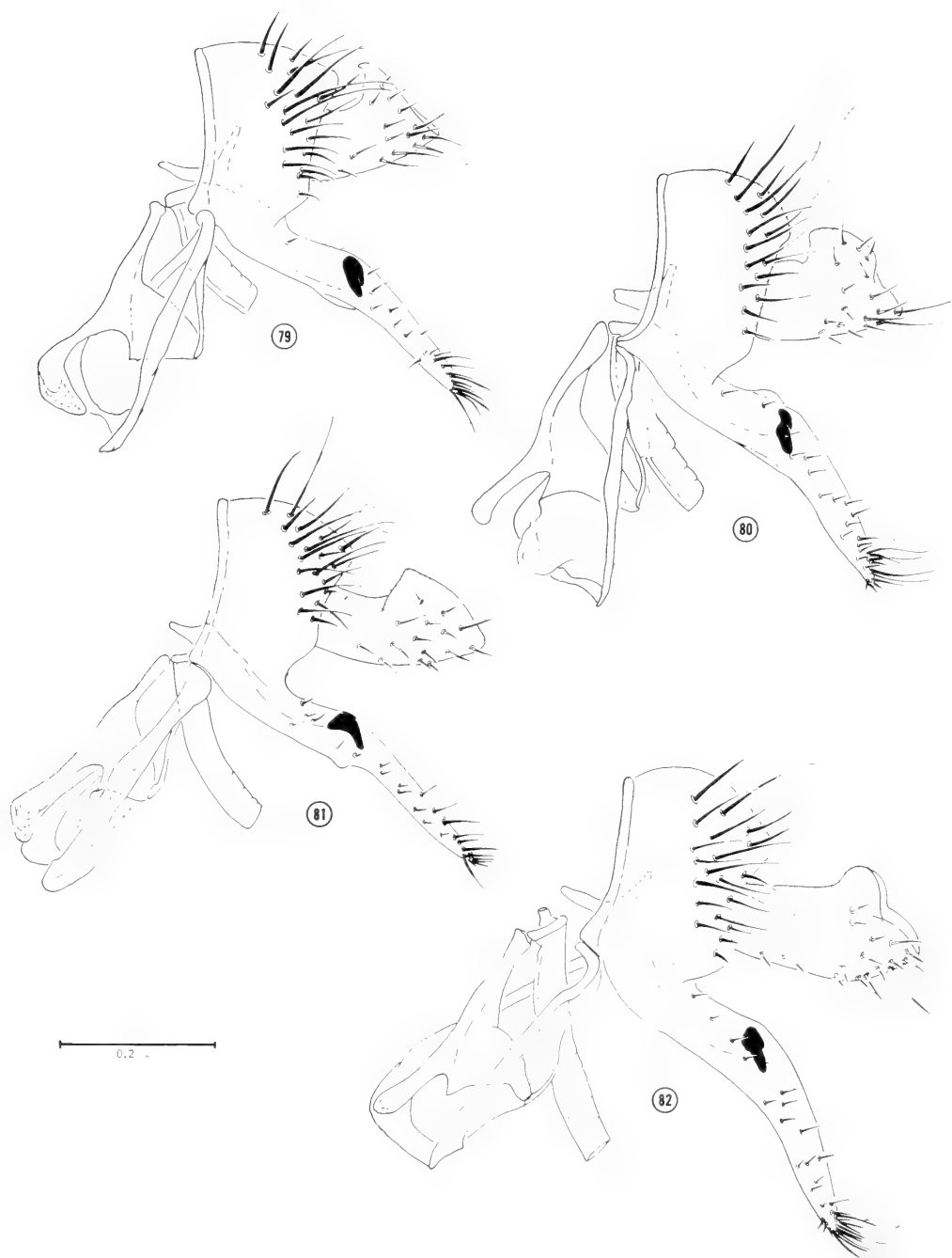
Figures 79–82. Lateral view of male genitalia of *Rhagoletis* species. Fig. 79. *R. cingulata* (Loew), Mass. Fig. 80. *R. chionanthi* n. sp., Fla. Fig. 81. *R. indifferens* Curran, Calif. Fig. 82. *R. osmanthi* n. sp., Fla.
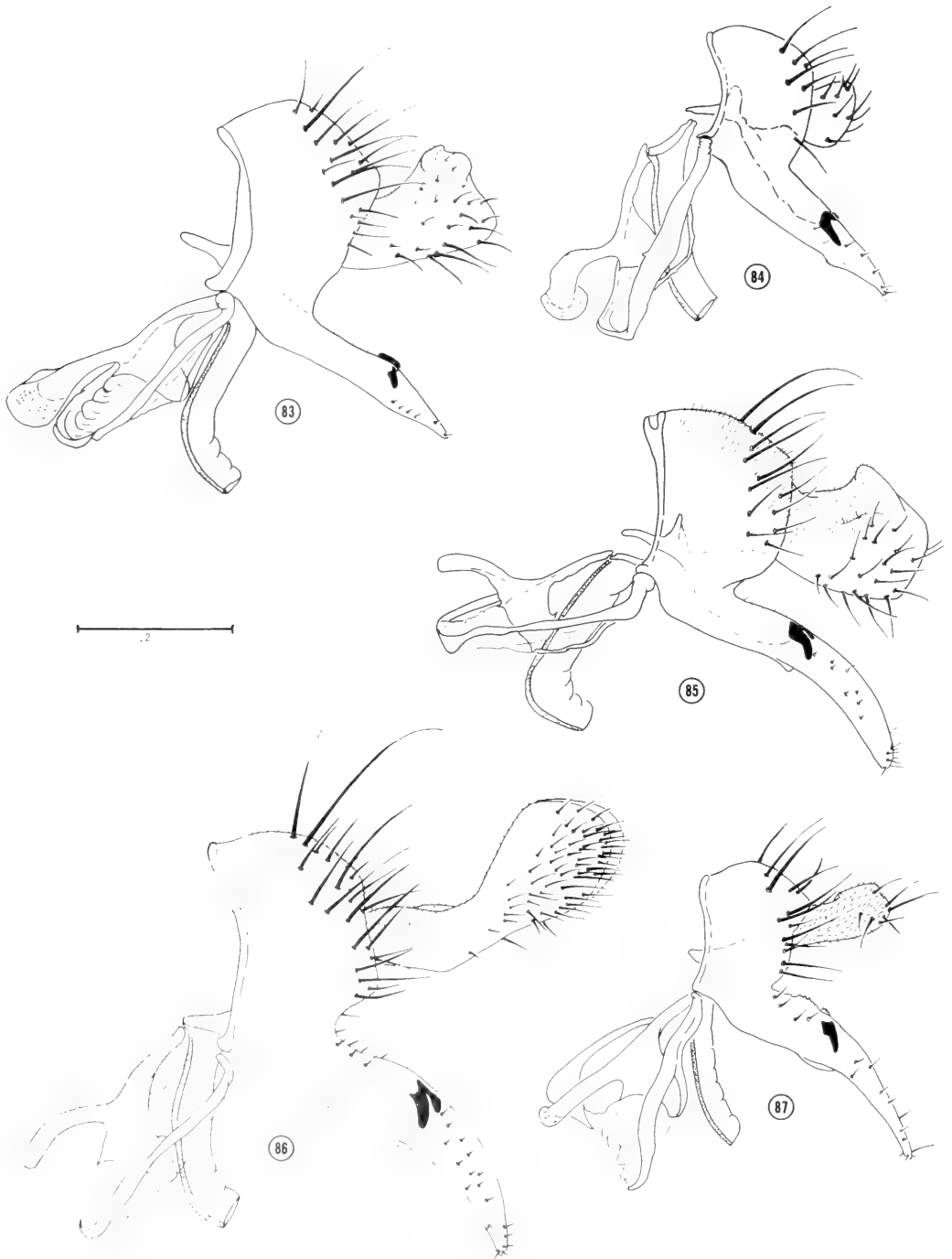
Figures 83–87. Lateral view of male genitalia of *Rhagoletis* species. Fig. 83. *R. juniperina* Marcovitch, Mass. Fig. 84. *R. ribicola* Doane, Ore. Fig. 85. *R. tabellaria* (Fitch), Mass. Fig. 86. *R. persimilis* n. sp., B.C., Can. Fig. 87. *R. berberis* Curran, Ore.
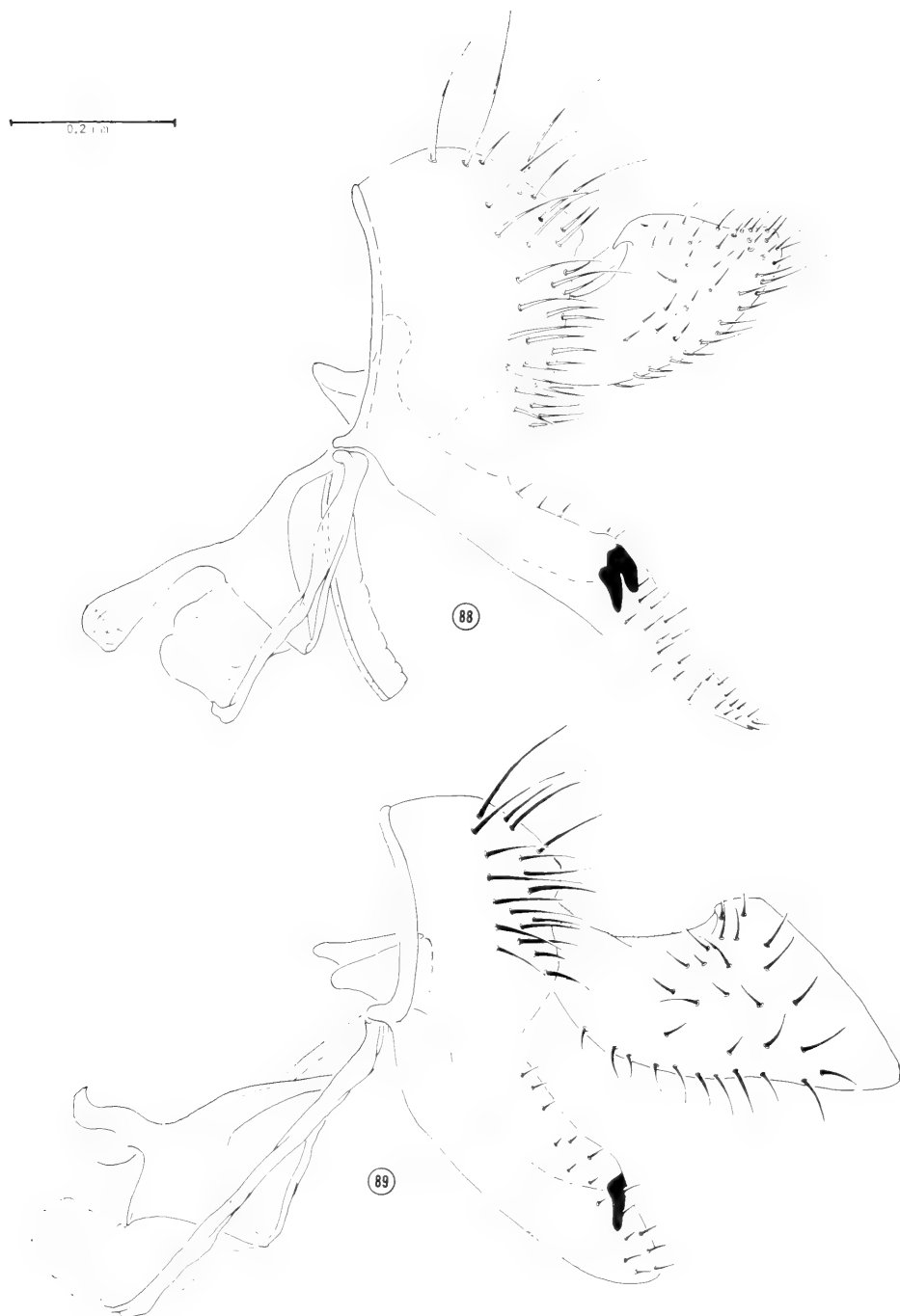
Figures 88–89. Lateral view of male genitalia of *Rhagoletis* species. Fig. 88. *R. basiola* (Osten Sacken), Mass. Fig. 89. *R. striatella* van der Wulp, Mexico.
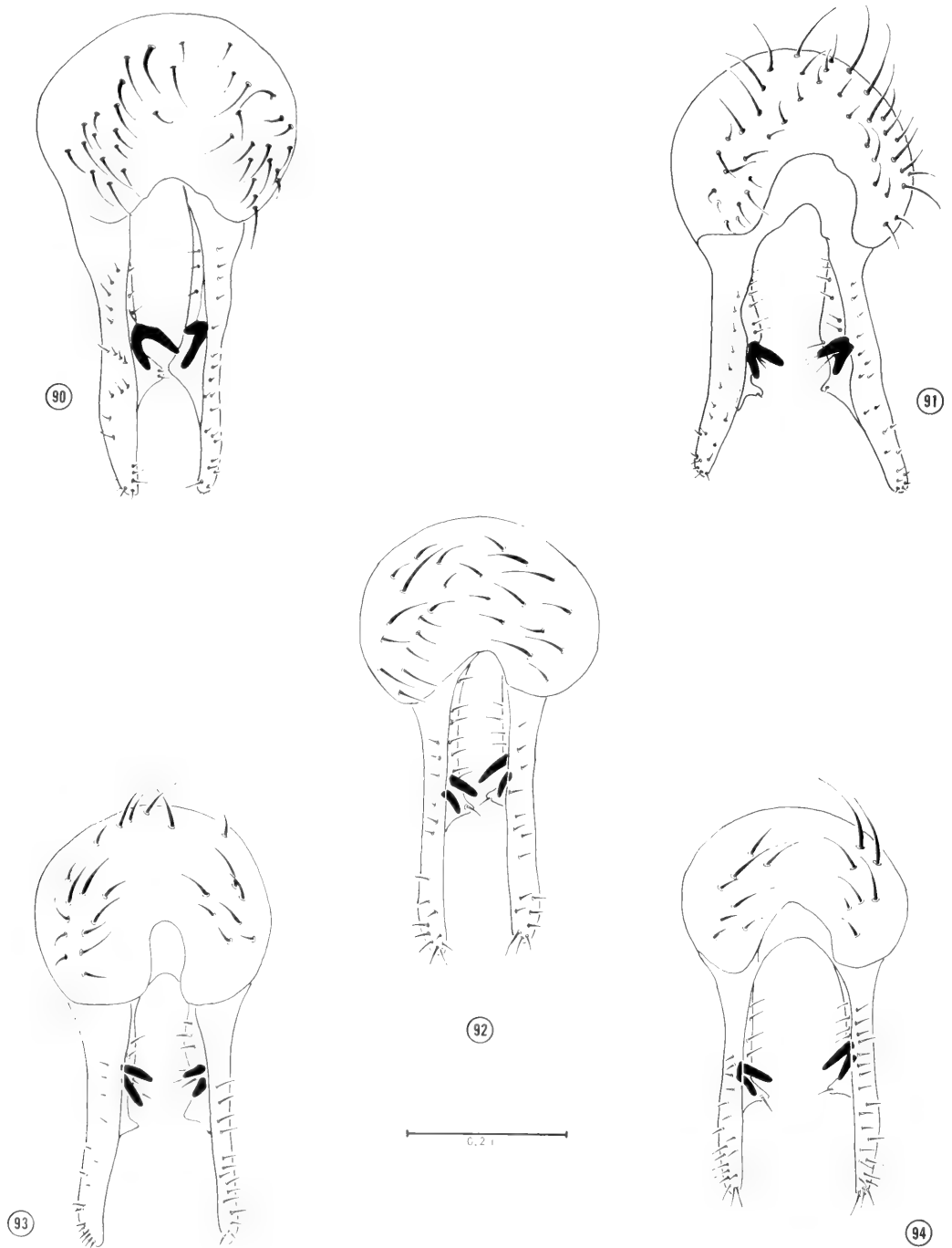
Figures 90–94. Posterior view of male genitalia of *Rhagoletis* species. Fig. 90. *R. pomonella* (Walsh), Mass. Fig. 91. *R. zephyria* Snow, Calif. Fig. 92. *R. cornivora* n. sp., Mass. Fig. 93. *R. mendax* Curran, Maine. Fig. 94. *R. mendax* Curran, Fla.
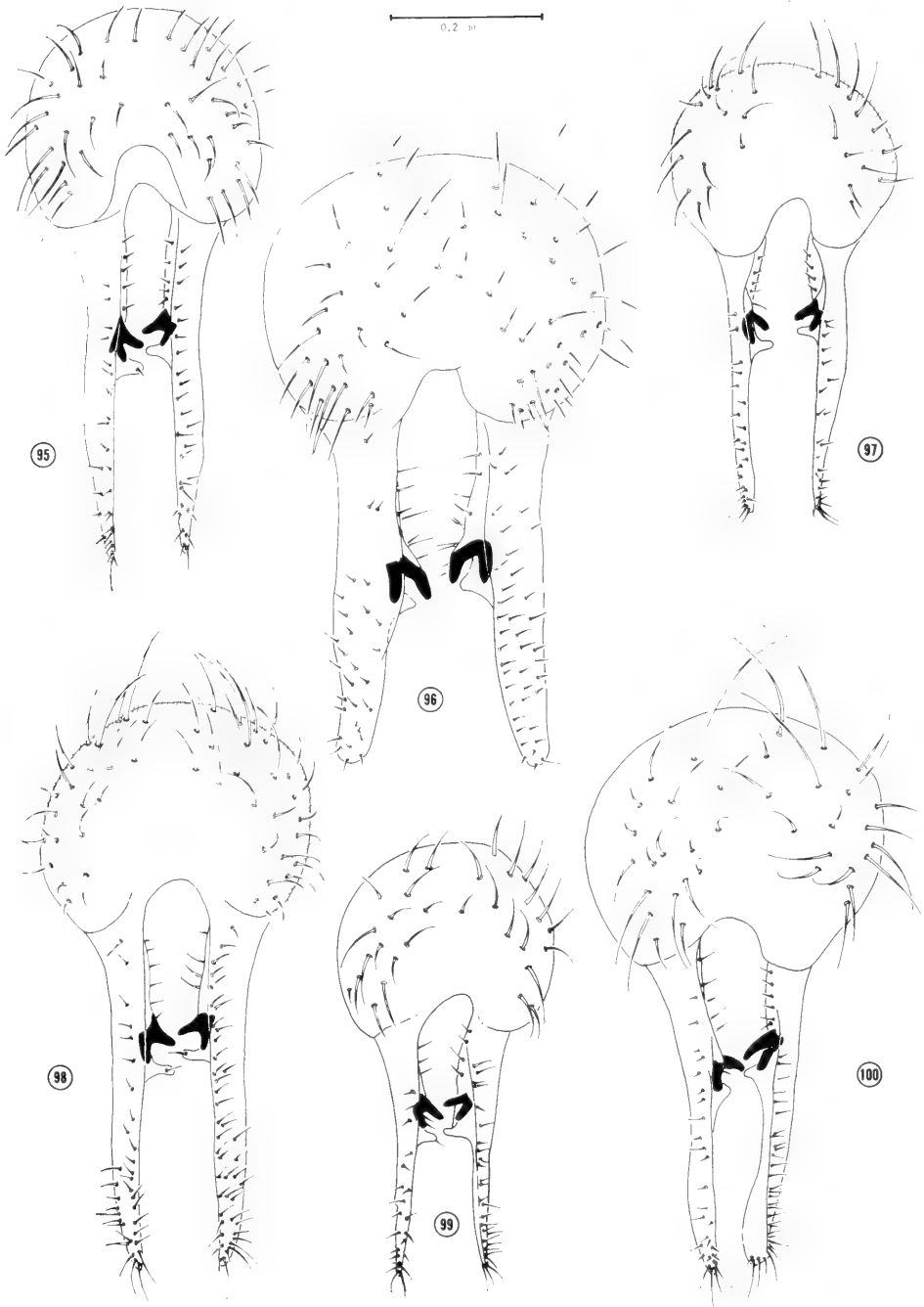
Figures 95–100. Posterior view of male genitalia of *Rhagoletis* species. Fig. 95. *R. boycei* Cresson, Ariz. Fig. 96. *R. basiola* (Osten Sacken), Mass. Fig. 97. *R. completa* Cresson, Calif. Fig. 98. *R. zoqui* n. sp., Hidalgo, Mex. Fig. 99. *R. juglandis* Cresson, Ariz. Fig. 100. *R. suavis* (Loew), Mass.
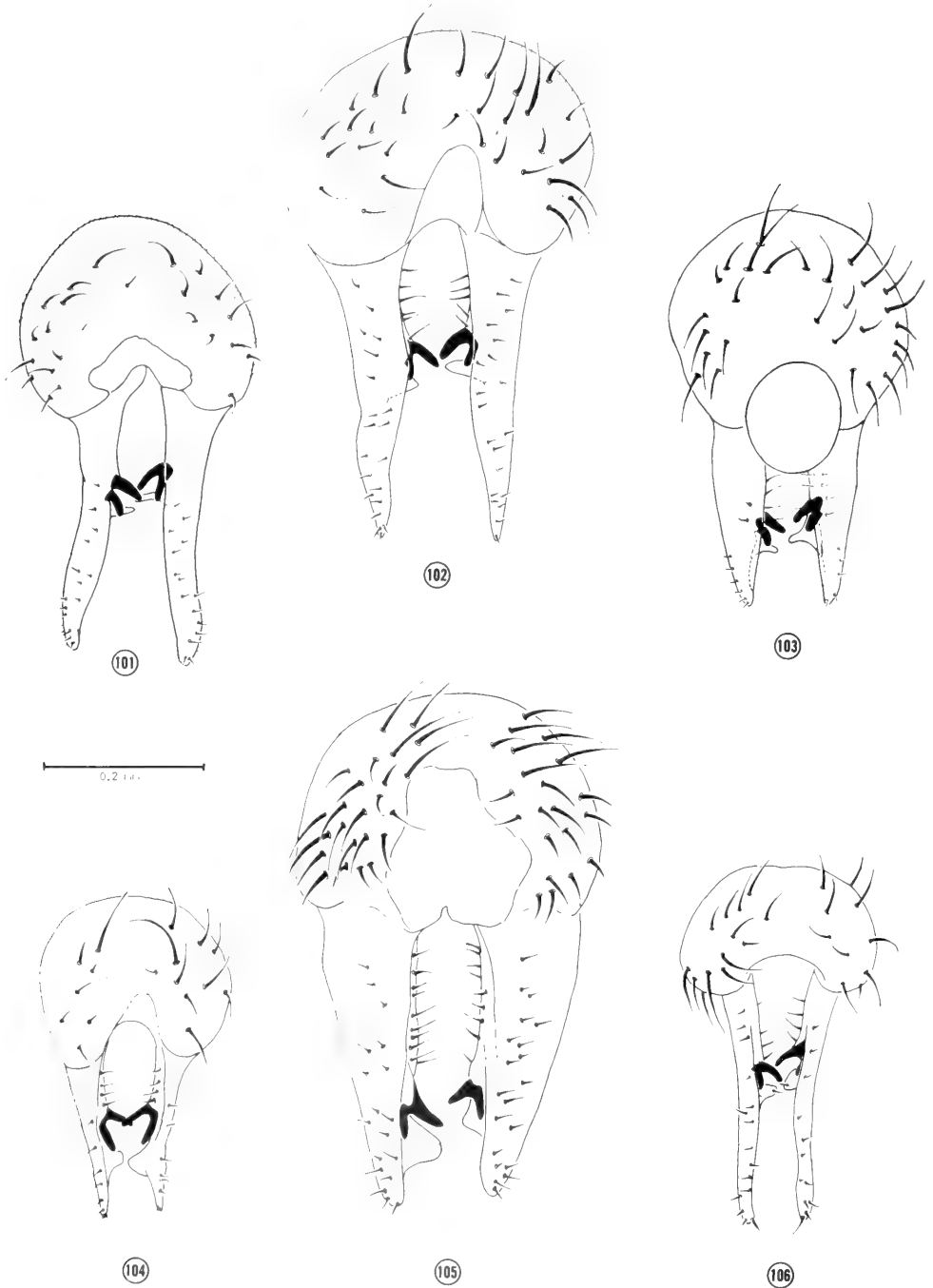
Figures 101–106. Posterior view of male genitalia of *Rhagoletis* species. Fig. 101. *R. tabellaria* (Fitch), Mass. Fig. 102. *R. persimilis* n. sp., B.C., Can. Fig. 103. *R. juniperina* Marcovitch, Mass. Fig. 104. *R. ribicola* Doane, Ore. Fig. 105. *R. striatella* van der Wulp, Mexico. Fig. 106. *R. berberis* Curran, Ore.
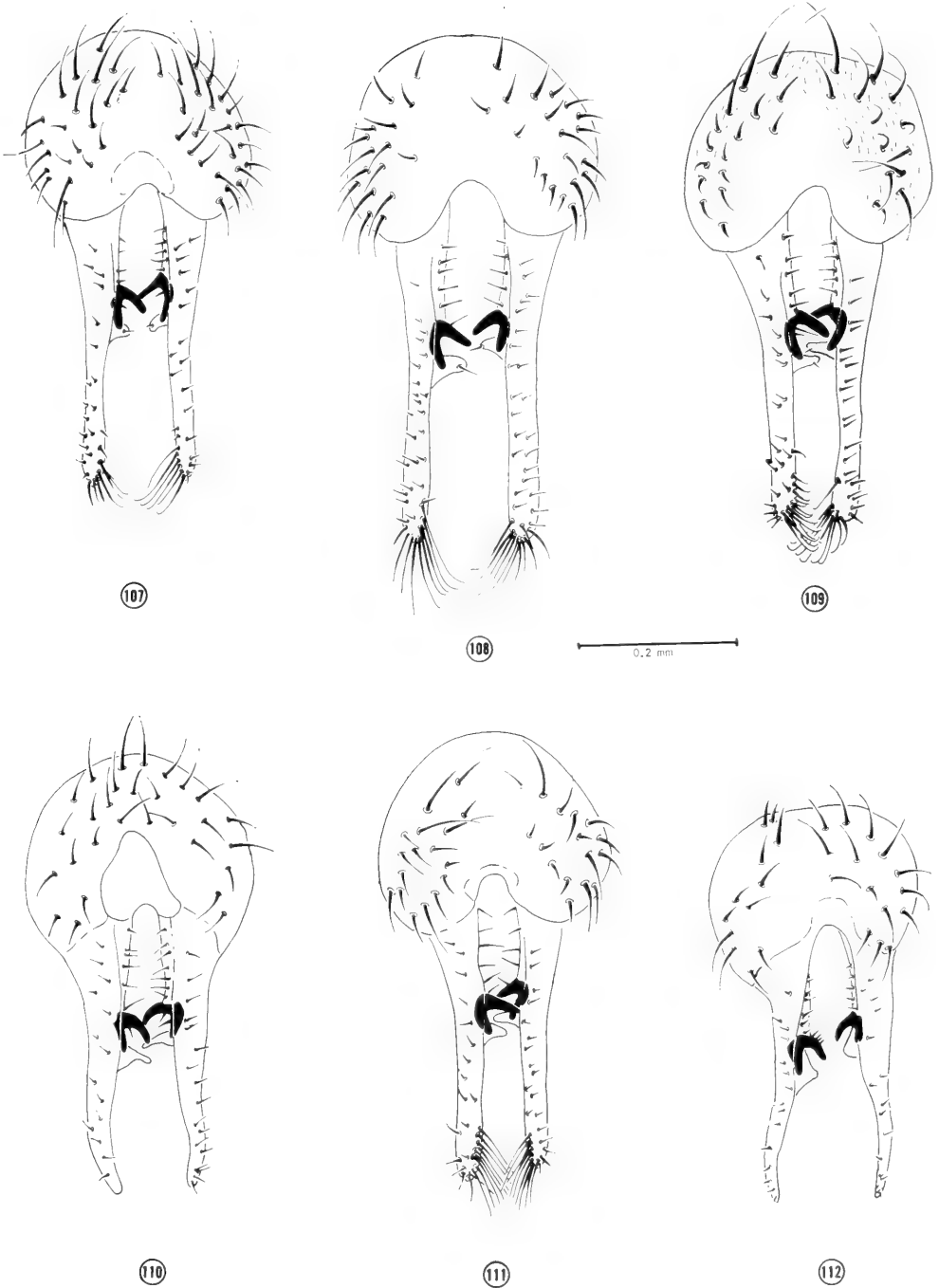
Figures 107–112. Posterior view of male genitalia of *Rhagoletis* species. Fig. 107. *R. indifferens* Curran, Calif. Fig. 108. *R. osmanthi* n. sp., Fla. Fig. 109. *R. chionanthi* n. sp., Fla. Fig. 110. *R. fausta* (Osten Sacken), N.H. Fig. 111. *R. cingulata* (Loew), Mass. Fig. 112. *R. cerasi* (Linn.), France.
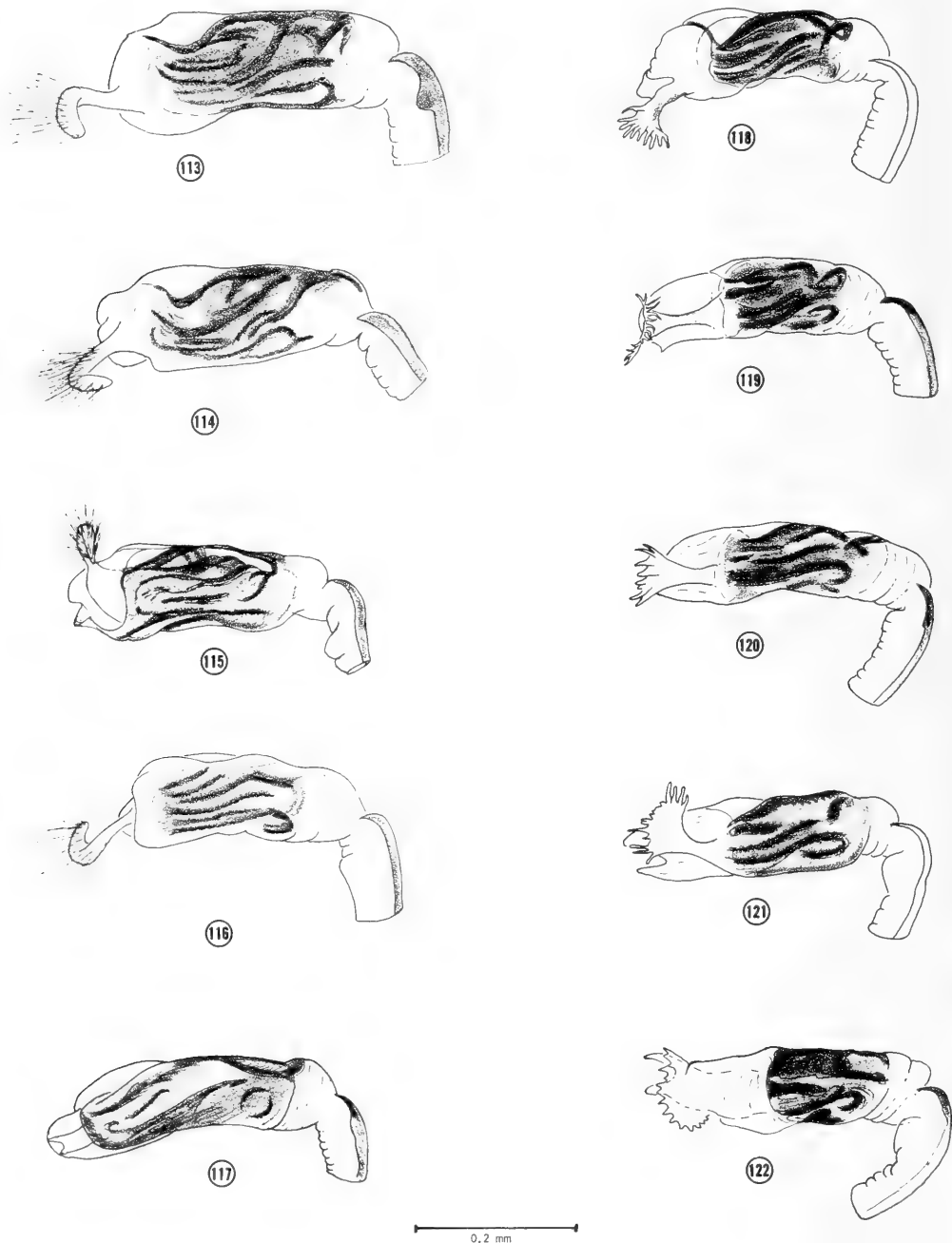
Figures 113–122. Lateral view of aedeagus of *Rhagoletis* species. Fig. 113. *R. pomonella* (Walsh), Mass. Fig. 114. *R. zephyria* Snow, Calif. Fig. 115. *R. mendax* Curran, Maine. Fig. 116. *R. cornivora* n. sp., Mass. Fig. 117. *R. fausta* (Osten Sacken), N.H. Fig. 118. *R. cingulata* (Loew), Mass. Fig. 119. *R. indifferens* Curran, Calif. Fig. 120. *R. osmanthi* n. sp., Fla. Fig. 121. *R. chionanthi* n. sp., Fla. Fig. 122. *R. cerasi* (Linn.), France.
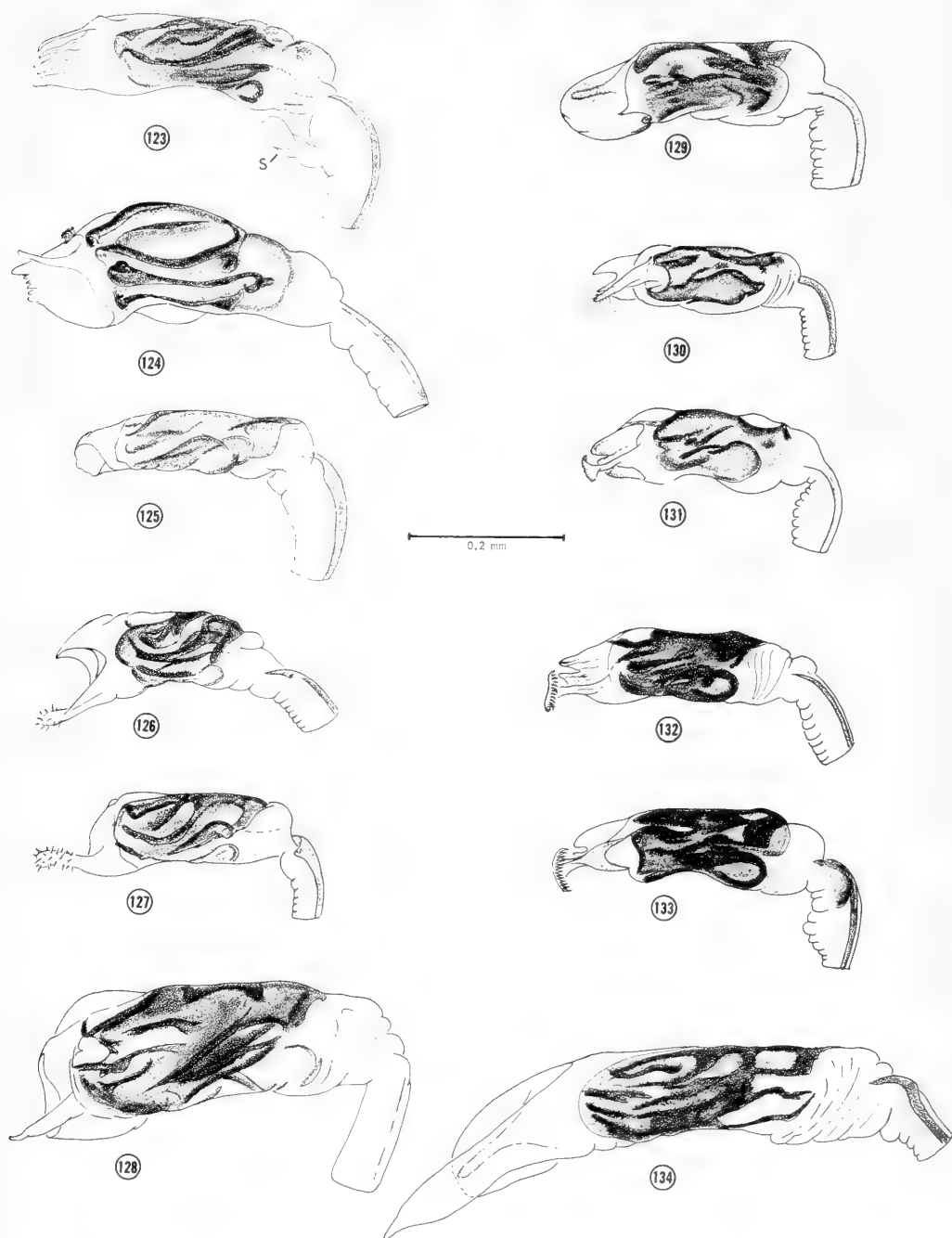
Figures 123–134. Lateral view of aedeagus of *Rhagoletis* species. Fig. 123. *R. tabellaria* (Fitch), Mass., S = tubular sac. Fig. 124. *R. persimilis* n. sp., B.C., Can. Fig. 125. *R. juniperina* Marcovitch, Mass. Fig. 126. *R. berberis* Curran, Ore. Fig. 127. *R. ribicola* Doane, Ore. Fig. 128. *R. basiola* (Osten Sacken), Mass. Fig. 129. *R. suavis* (Loew), Mass. Fig. 130. *R. juglandis* Cresson, Ariz. Fig. 131. *R. completa* Cresson, Calif. Fig. 132. *R. boycei* Cresson, Ariz. Fig. 133. *R. zoqui* n. sp., Hidalgo, Mex. Fig. 134. *R. striatella* van der Wulp, Mexico.
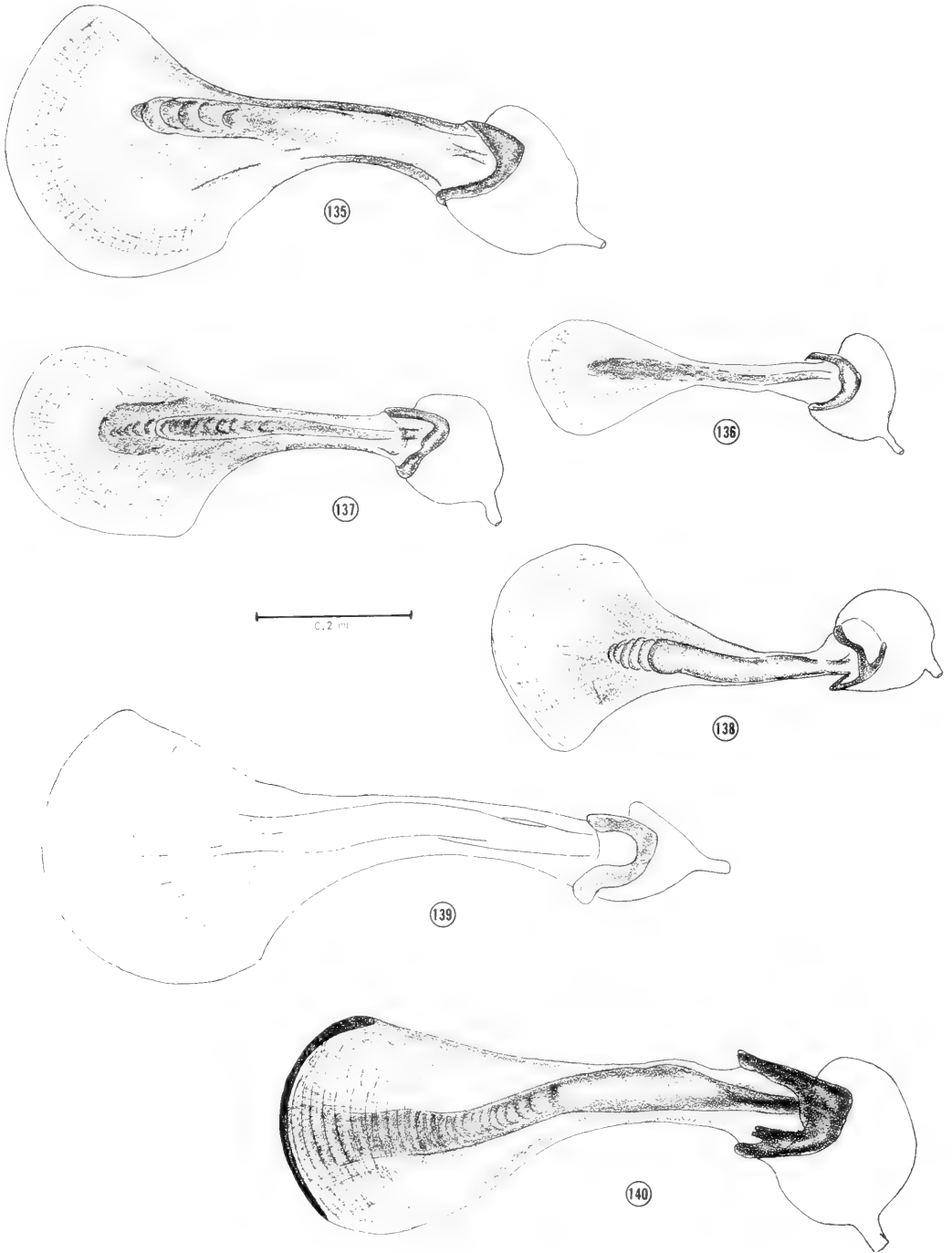
Figures 135–140. Ejaculatory apodeme of *Rhagoletis* species. Fig. 135. *R. pomonella* (Walsh), Mass. Fig. 136. *R. cornivora* n. sp., Mass. Fig. 137. *R. zephyria* Snow, Calif. Fig. 138. *R. mendax* Curran, Maine. Fig. 139. *R. basiola* (Osten Sacken), Mass. Fig. 140. *R. striatella* van der Wulp, Hidalgo, Mex.
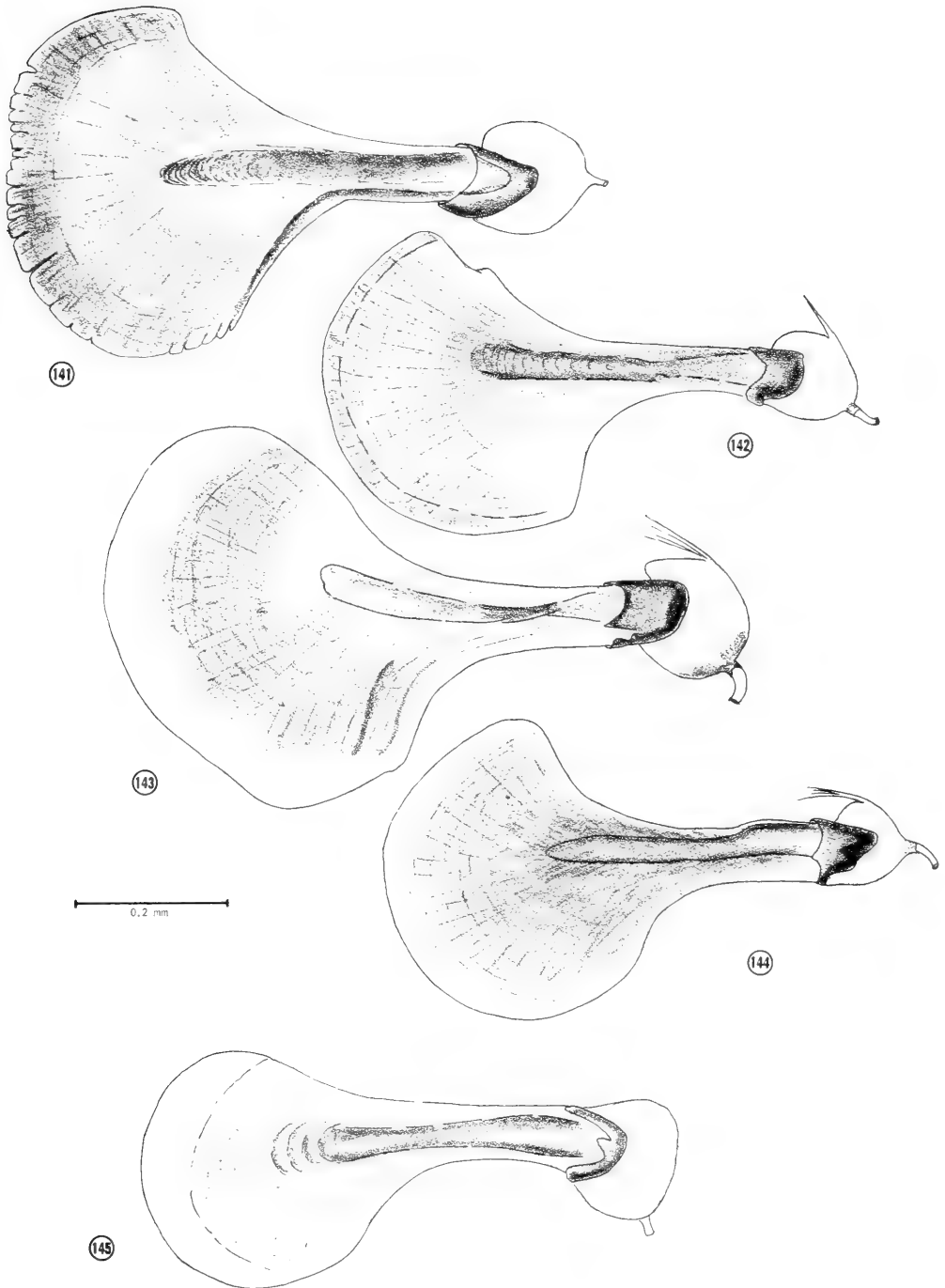
Figures 141–145. Ejaculatory apodeme of *Rhagoletis* species. Fig. 141. *R. suavis* (Loew), Mass. Fig. 142. *R. juglandis* Cresson, Ariz. Fig. 143. *R. zoqui* n. sp., Hidalgo, Mex. Fig. 144. *R. boycei* Cresson, Ariz. Fig. 145. *R. completa* Cresson, Calif.
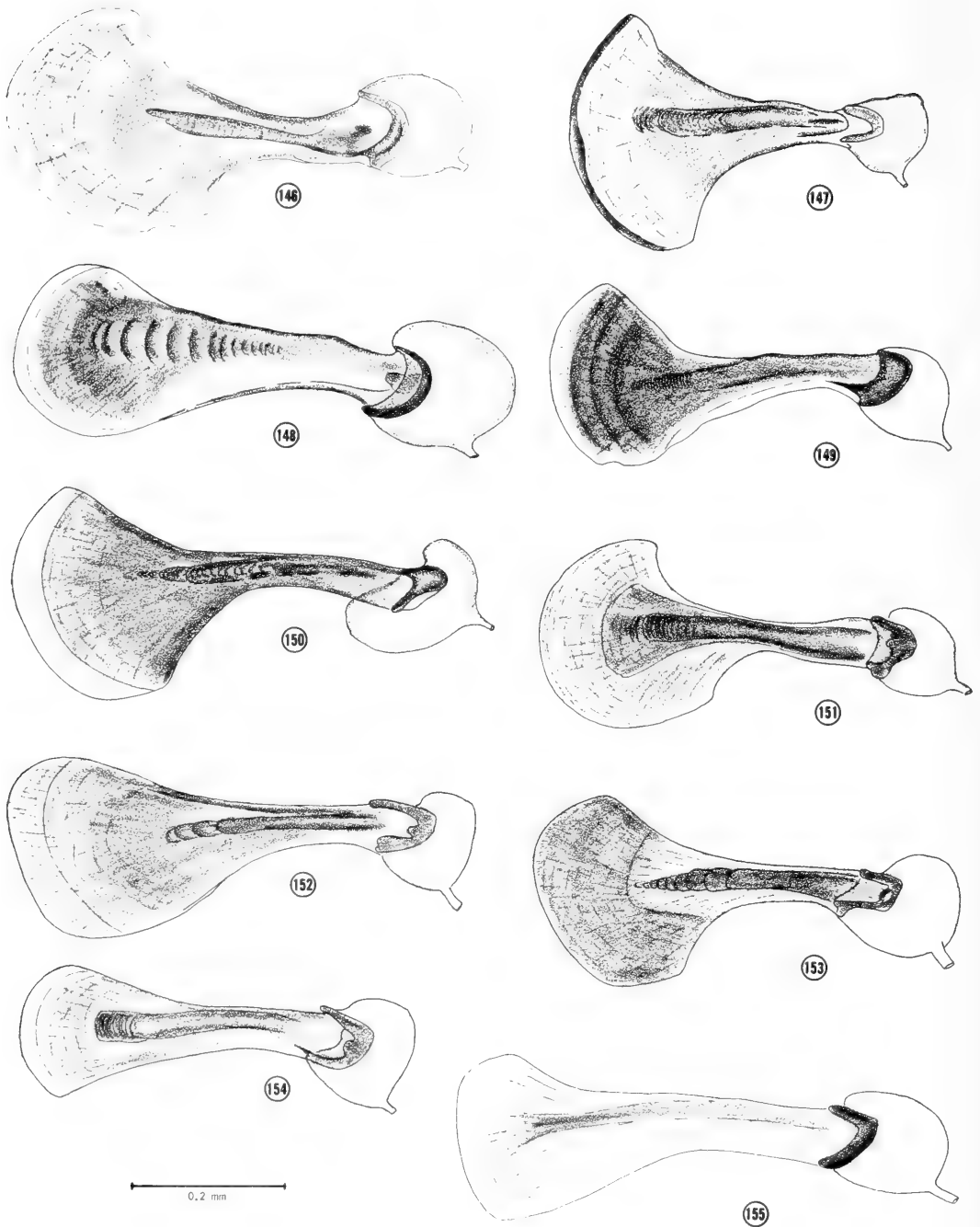
Figures 146–155. Ejaculatory apodeme of *Rhagoletis* species. Fig. 146. *R. tabellaria* (Fitch), Mass. Fig. 147. *R. ribicola* Doane, Ore. Fig. 148. *R. persimilis* n. sp., B.C., Can. Fig. 149. *R. berberis* Curran, Ore. Fig. 150. *R. juniperina* Marcovitch, Mass. Fig. 151. *R. fausta* (Osten Sacken), N.H. Fig. 152. *R. cingulata* (Loew), Mass. Fig. 153. *R. indifferens* Curran, Calif. Fig. 154. *R. chionanthi* n. sp., Fla. Fig. 155. *R. osmanthi* n. sp., Fla.
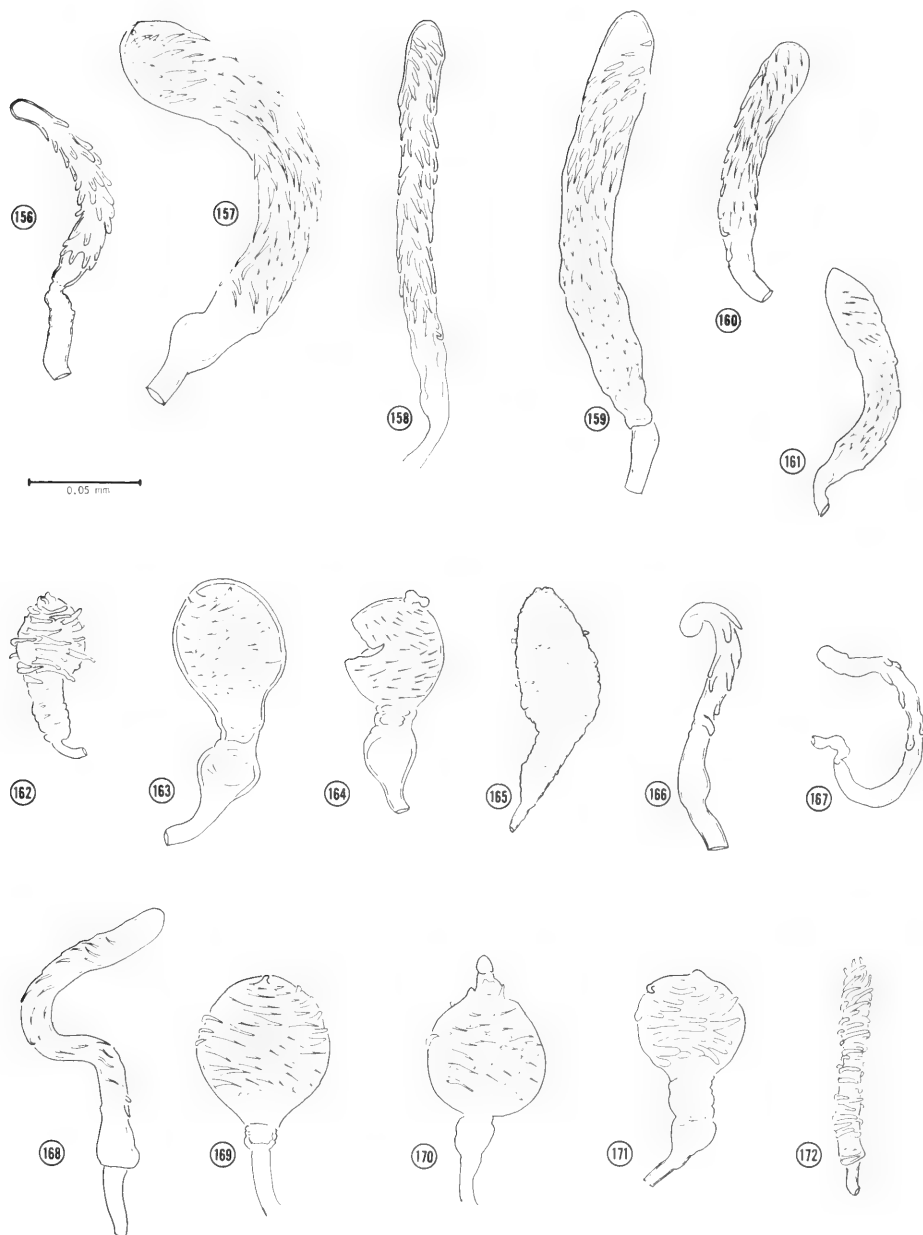
Figures 156–172. Spermathecae of *Rhagoletis* species. Fig. 156. *R. pomonella* (Walsh), Mass. (also typical of *mendax, zephyria* and *cornivora*). Fig. 157. *R. suavis* (Loew), Mass. Fig. 158. *R. completa* Cresson, Calif. Fig. 159. *R. zoqui* n. sp., Hidalgo, Mex. Fig. 160. *R. juglandis* Cresson, Ariz. Fig. 161. *R. boycei* Cresson, Ariz. Fig. 162. *R. tabellaria* (Fitch), Mass. Fig. 163. *R. juniperina* Marcovitch, Mass. Fig. 164. *R. ebbettsi* n. sp. (holotype), Calif. Fig. 165. *R. persimilis* n. sp., B.C., Can. Fig. 166. *R. berberis* Curran, Ore. Fig. 167. *R. ribicola* Doane, Ore. Fig. 168. *R. cingulata* (Loew), Mass. (also typical of *indifferens, osmanthi* and *chionanthi*). Fig. 169. *R. basiola* (Osten Sacken), Mass. Fig. 170. *R. striatella* van der Wulp, Mexico. Fig. 171. *R. fausta* (Osten Sacken), N.H. Fig. 172. *R. cerasi* (Linn.), France.
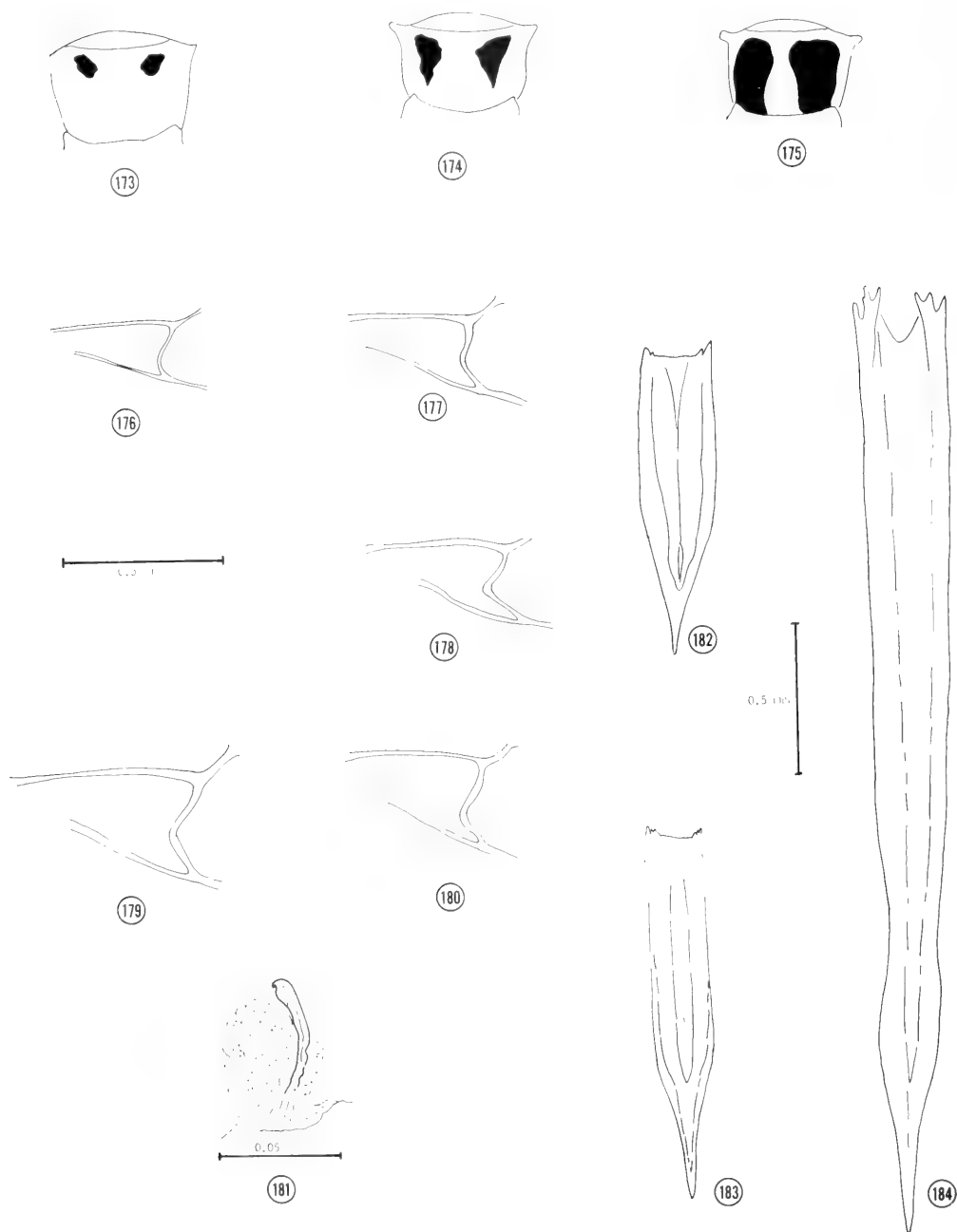
Figures 173–175. Postscutellum of *Rhagoletis* species. Fig. 173. *R. basiola* (Osten Sacken), ♂, Minn. Fig. 174. *R. basiola* (Osten Sacken), ♂, Minn. Fig. 175. *R. alternata* (Fallen), ♂, Germany. Figures 176–180. Anal cell of *Rhagoletis* species. Fig. 176. *R. ribicola* Doane, Ore. Fig. 177. *R. berberis* Curran, Ore. Fig. 178. *R. juniperina* Marcovitch, Mass. Fig. 179. *R. persimilis* n. sp., B.C., Can. Fig. 180. *R. tabellaria* (Fitch), Mass. Figure 181. Ventral receptacle of *R. cerasi* (Linn.), France. Figures 182–184. Ovipositor of *Rhagoletis* species. Fig. 182. *R. basiola* (Osten Sacken), Mass. Fig. 183. *R. pomonella* (Walsh), Mass. Fig. 184. *R. striatella* van der Wulp, Mexico.
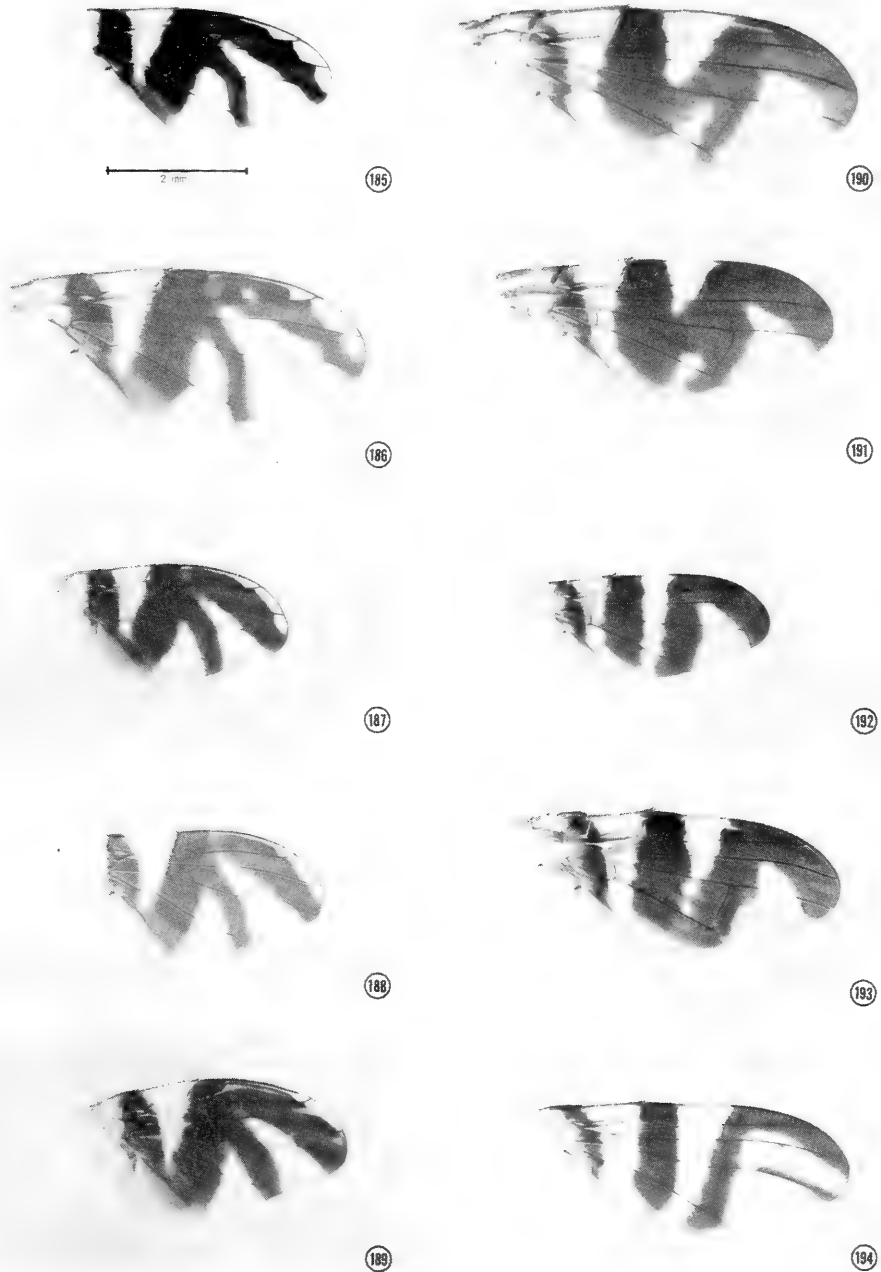
Figures 185–194. Wing pattern of *Rhagoletis* species. Fig. 185. *R. pomonella* (Walsh), ♂, N.S., Can. Fig. 186. *R. pomonella* (Walsh), ♀, Mexico. Fig. 187. *R. zephyria* Snow, ♂, B.C., Can. Fig. 188. *R. mendax* Curran, ♀, Maine. Fig. 189. *R. cornivora* n. sp., ♀, Mass. Fig. 190. *R. suavis* (Loew), ♂, Kans. Fig. 191. *R. suavis* (Loew), ♀, Mich. Fig. 192. *R. completa* Cresson, ♀, Calif. (normal pattern). Fig. 193. *R. completa* Cresson, ♀, Calif. (abnormal pattern). Fig. 194. *R. boycei* Cresson, ♀, N.M.

Figures 195–204. Wing pattern of *Rhagoletis* species. Fig. 195. *R. juglandis* Cresson, ♀, Ariz. Fig. 196. *R. zoqui* n. sp., ♂, Hidalgo, Mex. Fig. 197. *R. tabellaria* (Fitch), ♂, Mass. Fig. 198. *R. juniperina* Marcovitch, ♀, Mass. Fig. 199. *R. persimilis* n. sp., ♀, B.C., Can. Fig. 200. *R. ebbettsi* n. sp., ♀ (holotype), Calif. Fig. 201. *R. ribicola* Doane, ♀, Ore. Fig. 202. *R. berberis* Curran, ♂, Ore. Fig. 203. *R. cingulata* (Loew), ♀, Fla. Fig. 204. *R. indifferens* Curran, ♂, Wash. (normal pattern).
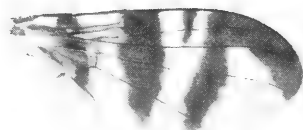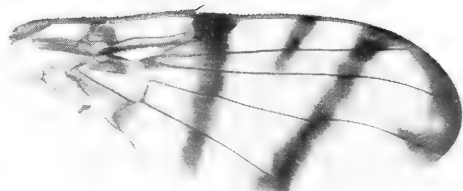
Figures 205–212. Wing pattern of *Rhagoletis* species. Fig. 205. *R. indifferens* Curran, ♂, Calif. (abnormal pattern). Fig. 206. *R. osmanthi* n. sp., ♀, Fla. Fig. 207. *R. chionanthi* n. sp., ♀, Fla. Fig. 208. *R. alternata* (Fallen), ♀, Germany. Fig. 209. *R. striatella* van der Wulp, ♀, Hidalgo, Mex. Fig. 210. *R. fausta* (Osten Sacken), ♀, N.H. Fig. 211. *R. cerasi* (Linn.), ♀, France. Fig. 212. *R. basiola* (Osten Sacken), ♀, Mass.

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Figures 213–232. Chromosomes from anterior ganglia of larvae of *Rhagoletis* species. (Unless otherwise stated, sex unknown.) Fig. 213. *R. pomonella*, metaphase; ex *Pyrus Malus*, N.S., Can. Fig. 214. *R. pomonella*, anaphase; ex *Pyrus malus*, N.S., Can. Fig. 215. *R. zephyria*, late metaphase; ex *Symphoricarpos* sp., Ore. Fig. 216. *R. mendax*, metaphase; ex *Vaccinium* sp., N.H. Fig. 217. *R. cornivora*, ♂, metaphase; ex *Cornus amomum*, Mass. Fig. 218. *R. suavis*, metaphase; ex *Juglans cinerea*, Mass. Fig. 219. *R. suavis*, anaphase; ex *Juglans cinerea*, Mass. Fig. 220. *R. completa*, metaphase, ex *Juglans* sp., Calif. Fig. 221. *R. juglandis*, metaphase; ex *Juglans major*, Ariz. Fig. 222. *R. boycei*, metaphase; ex *Juglans major*, Ariz. Fig. 223. *R. zoqui*, metaphase; ex *Juglans mollis*, Hidalgo, Mex. Fig. 224. *R. cingulata*, metaphase, ex *Prunus serotina*, N.H. Fig. 225. *R. indifferens*, metaphase; ex *Prunus emarginata*, Calif. Fig. 226. *R. tabellaria*, metaphase; ex *Vaccinium* sp., Wash. Fig. 227. *R. juniperina*, metaphase; ex *Juniperus virginiana*, Mass. Fig. 228. *R. ribicola*, metaphase; ex *Ribes* sp., Ore. Fig. 229. *R. berberis*, ♀, metaphase; ex *Mahonia nervosa*, Ore. (SAT = satellite). Fig. 230. *R. berberis*, ♂, metaphase; ex *Mahonia nervosa*, Ore. Fig. 231. *R. basiola*, metaphase; ex *Rosa* sp., Mass. Fig. 232. *R. basiola*, anaphase; ex *Rosa* sp., Mass.
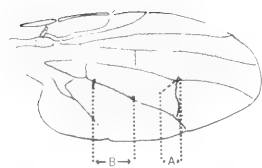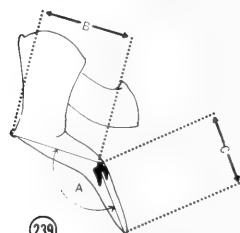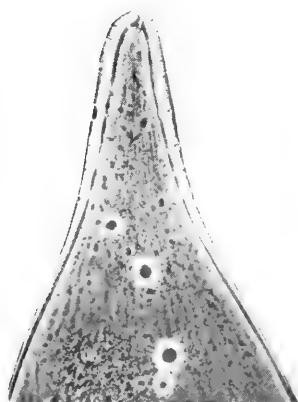
Figures 233–237. Chromosomes from anterior ganglia of larvae of *Rhagoletis* species. (Unless otherwise stated, sex unknown.) Fig. 233. *R. basiola,* late prophase; ex *Rosa* sp., Mass. Fig. 234. *R. striatella,* metaphase; ex *Physalis* sp., Mexico, Mex. (SAT = satellite). Fig. 235. *R. striatella,* anaphase; ex *Physalis* sp., Mexico, Mex. Fig. 236. *R. fausta,* metaphase; ex *Prunus pennsylvanica,* Mass. Fig. 237. *R. fausta,* early anaphase; ex *Prunus pennsylvanica,* Mass. Fig. 238. Method for measuring wing band ratio in the *pomonella* species group. Fig. 239. Method for measuring surstylus ratio and angle in the *pomonella* species group. Fig. 240. Micropyle of egg of *R. striatella* van der Wulp. Fig. 241. Micropyle of egg of *R. pomonella* (Walsh).

Date Due